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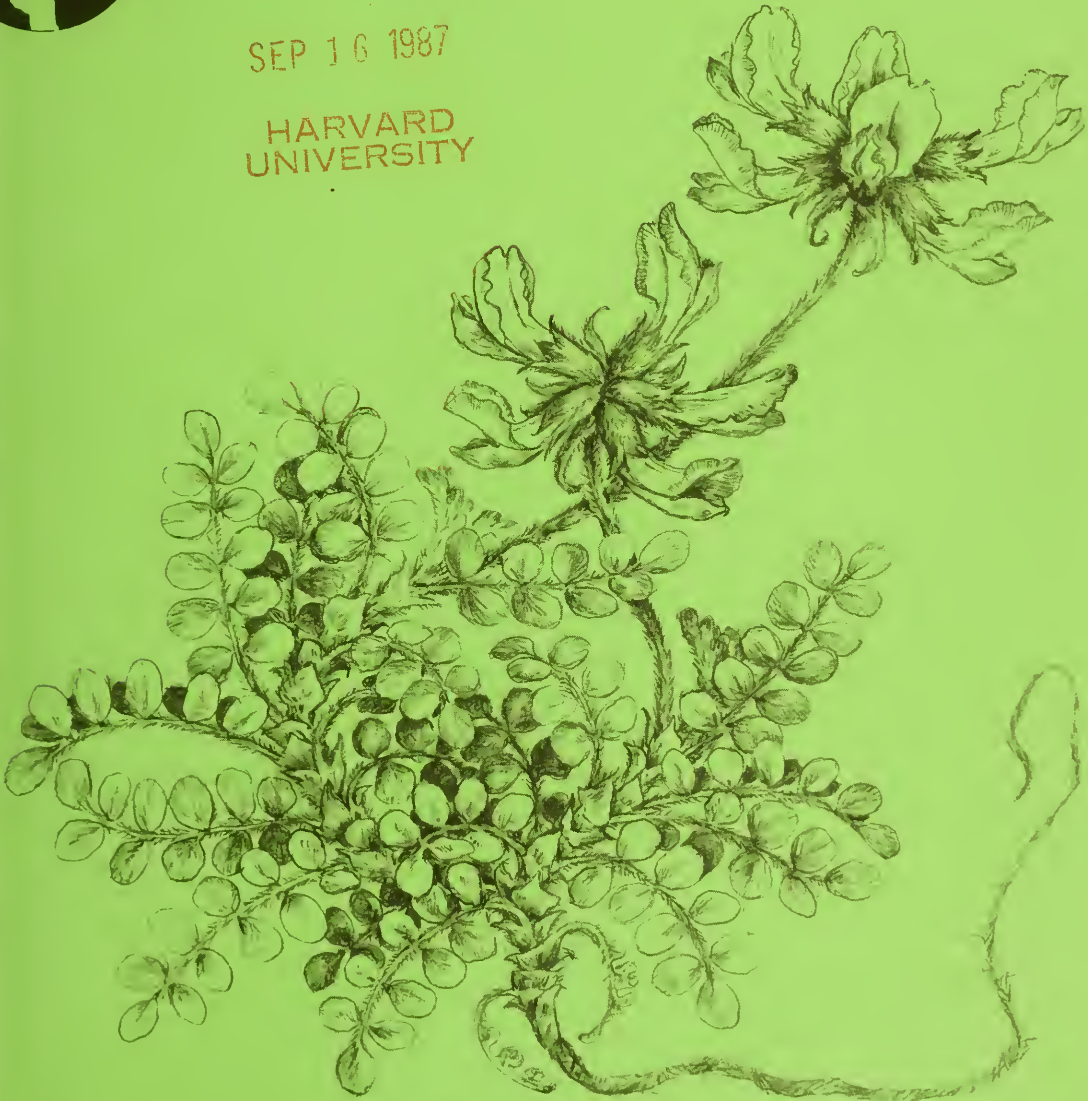

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COMPETITION FOR FOOD AND SPACE IN A HETEROMYID COMMUNITY IN THE GREAT BASIN DESERT

Cliff A. Lemen[1] and Patricia W. Freeman[1]

Abstract.—A series of removal experiments were performed on *Dipodomys merriami*, *D. microps*, and *Perognathus longimembris* to test for the importance of competition for food and microhabitats in a heteromyid community in the Great Basin Desert. Each of these species was removed singly to determine the short-term effects on the microhabitat preferences of the remaining species. We correctly predicted, based on differences in diet, that the removal of *D. microps* (a foliovore) would have no effect on *D. merriami* or *P. longimembris* (granivores). Using the dominance hierarchy theory, we correctly predicted that removal of a larger heteromyid, *D. merriami*, would have an effect on the microhabitat use of the smaller *P. longimembris*, but not vice versa. While our results offer strong evidence of competition for food and microhabitats, the short-term reactions were weak compared to the long-term reactions found in other studies of heteromyids.

When a competitor is removed from a community, the remaining species can react by an increase in density, a shift in the use of resources, or both. These reactions are evidence of competition, but they connote different aspects of the competitive interaction. Changes in densities indicate the strength of competition. Shifts in the use of resources indicate which resources are competed for and how competition has altered the fundamental niches of competitors.

Food and microhabitats have been proposed as the resources that are competed for by heteromyids (Rosenzweig 1973, Brown 1975). We tested for the intensity of this competition with a large-scale experiment that measured both changes in numbers of animals and use of resources when species were removed. This paper deals with changes in the use of resources after a perturbation. A companion paper (Lemen and Freeman 1986) discusses the density responses to the removals.

Our criteria for the presence of competition are changes in the use of microhabitats after species are removed. The use of changes in microhabitats as our test for competition is based on the success of removal experiments by Price (1978) and Wondolleck (1978). These studies showed short-term shifts in foraging patterns in heteromyids. We were particularly interested in repeating some of Price and Wondolleck's work because their results indicated that larger heteromyids have a short-term response to the removal of smaller heteromyids. This result is inconsistent with our view of a dominance hierarchy based on size (Lemen and Freeman 1983, O'Farrell 1980, Frye 1983). Lemen and Freeman (1983) maintained that short-term removals of a few weeks would not be long enough to affect resource levels. Any reaction to the removal is probably a direct response to the absence of the competitor and not a reaction mediated by changes in resources. Behavioral work (Blaustein 1974, Congdon 1974, Eisenberg 1963) indicates that heteromyids are highly aggressive both intra- and interspecifically. We hypothesized that this aggression might be the basis of a dominance hierarchy in which large species compelled small species to reduce their use of some microhabitats. The dominance hierarchy hypothesis predicts that removal of large, aggressive heteromyids will produce a short-term shift in use of microhabitats by smaller heteromyids, but that removal of small, subordinate species will not produce a short-term reaction by larger species.

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To test our next hypothesis, that heteromyids compete for food, we removed granivorous and nongranivorous species and quantified the reaction of the remaining species. The experiment is similar to that used by Munger and Brown (1981) and Brown and Munger (1985), who noted that the removal of granivores (*Dipodomys*) produced an increase in density of granivorous species (*Perognathus*) but produced no increase in density of nongranivorous species (*Onychomys* and *Neotoma*: Cricetidae). We were able to make this comparison within the Heteromyidae by taking advantage of the evolutionary shift in diet of *D. microps*. *Perognathus* and *Dipodomys* typically have similar diets of seeds and insects. *Dipodomys microps* is an exception to this dietary rule because it is folivorous and has little dietary overlap with the granivorous *P. longimembris* and *D. merriami* (Kenagy 1972). *Dipodomys microps* should not have to adjust its use of microhabitats to avoid competition with *P. longimembris* and *D. merriami*. Likewise, these seed-eating heteromyids would not be subject to the same competitive pressure to forage in different microhabitats when coexisting with *D. microps* as they would when coexisting with more conventional granivorous heteromyids. A study of the reaction of rodents to *D. microps* is the analog in evolutionary time of the removal of species in ecological time. In both cases the idea is to determine how the community responds when a species is removed, either by the removal of a species in ecological time or by the shift of a species to a new and nonoverlapping diet in evolutionary time.

MATERIALS AND METHODS

The study area is located near Goldfield, Nevada, at an elevation of 1,530 m in the Tonopah section of the Great Basin Desert (Cronquist et al. 1972). Rainfall averages 11.5 cm per year. Vegetation is dominated by shadscale (*Atriplex confertifolia*). Other common shrubs include *A. canescens*, *Sarcobatus vermiculatus*, *Kochia americana*, and *Lycium cooperi*. As is typical of this area, the cover of forbs and grasses is low. The entire area is grazed by cattle and wild horses.

During the summers of 1980 and 1981 trapping grids were established at the study site. We used 10 grids in the first year and 13 grids in the second year. Each grid was a 210-m square (4.4 ha) with trap stations at 15-m intervals, for a total of 225 trap stations per grid. Sherman live traps (7.5 x 23 cm), baited with mixed bird seed, were used. The grids were trapped from June 6 to August 18 in 1980 and from June 2 to July 8 in 1981. This produced a total of 36,000 trap-nights.

The grids were divided into controls and treatment plots. On the two control grids there were no removals, but the controls were trapped at the same interval as the other grids. There were four experimental treatments: removal of *D. microps*, removal of *D. merriami*, removal of both species of *Dipodomys*, and the removal of *P. longimembris*. All of these treatments were replicated twice the first summer and at least twice the second summer.

All grids were initially censused with two nights of trapping, and estimates of the initial number of animals on the grids were obtained using the Jolly method (White 1971). Each animal captured was identified, sexed, weighed, and given a unique eartag (monel fingerling tag). We immediately released the rodents on the control grids. Animals to be removed were turned loose about eight km away; no animal that had been removed from a grid ever returned. At approximately seven-day intervals we trapped each grid to maintain the removals.

The use of habitats was quantified by placing each trap in a specific microhabitat. The three microhabitats used were bush, near a bush (0.33 m of bush), or in the open (greater than 0.33 m of bush, but placed to maximize the distance to the nearest bush). The traps, when being set, were alternated among the microhabitats in a regular pattern. This meant that 75 traps were placed in each of the three microhabitats.

TABLE 1. The number of captures of rodents in each microhabitat in situations with no removals. Chi^2 values are from a goodness-of-fit test comparing the actual use of the open and bush microhabitats by each rodent to equal use of both microhabitats.

		Microhabitats			
		Bush	Near	Open	Chi^2
P. longimembris	year 1	235 (.56)	213	187 (.44)	5.46*
	year 2	197 (.54)	161	170 (.46)	1.99
D. merriami	year 1	260 (.47)	258	295 (.53)	2.21
	year 2	115 (.44)	123	148 (.56)	4.14*
D. microps	year 1	90 (.49)	104	93 (.51)	0.05
	year 2	78 (.42)	95	109 (.58)	5.14*

TABLE 2. The number of captures of rodents in each microhabitat in situations of intraspecific removals. Chi^2 values are from a contingency test comparing the use of the bush and open microhabitats by species with and without intraspecific removals.

		Microhabitats			
		Bush	Near	Open	Chi^2
P. longimembris	year 1	123	118	98	0.00
	year 2	49	37	27	2.97
D. merriami	year 1	68	93	81	0.07
	year 2	18	14	17	0.74
D. microps	year 1	14	20	22	1.28
	year 2	16	16	16	0.77

TABLE 3. The number of captures of rodents in each microhabitat in situations with interspecific removals. Chi^2 values are from a contingency test comparing the use of the bush and open microhabitats by species with and without interspecific removals.

			Microhabitats			
			Bush	Near	Open	Chi^2
P. longimembris	year 1	-*D. mer*	129	130	149	5.79*
		-*D. mic*	116	109	94	0.01
	year 2	-*D. mer*	32	32	39	1.77
		-*D. mic*	20	15	20	0.20
D. merriami	year 1	-*P. long*	93	100	95	0.49
		-*D. mic*	45	54	47	0.18
	year 2	-*P. long*	12	24	25	1.69
		-*D. mic*	21	19	34	0.57
D. microps	year 1	-*P. long*	116	91	94	1.44
		-*D. mer*	45	54	47	0.00
	year 2	-*P. long*	14	29	29	1.22
		-*D. mer*	27	18	25	1.72

RESULTS

Analysis of the preferences in microhabitat was performed on the 5,821 captures of three species (Tables 1, 2, 3). We used the capture data from control grids and the initial census data to estimate microhabitat preferences. These preferences were used to test the hypothesis that the rodents foraged equally in all microhabitats. Although we report use of the near microhabitat, we used only open and bush, the two extreme microhabitats, for the statistical tests. In 1980 *P. longimembris* was the only species that deviated from random

TABLE 4. Spatial patterns of distribution for the three most common heteromyids on control grids during summer of 1980 (because of the small number of *P. longimembris* on control grid #3, two other grids where this species was more abundant are substituted). Chi^2 values are generated by comparing the actual nearest neighbor distance to those expected by a random pattern of distribution. In all cases where a significant deviation from random occurs it is caused by hyperdispersion and not by clumping.

INTRASPECIFIC	grid	n	Chi^2	df	p
P. longimembris	7	40	10.01	2	< 0.01
	9	35	8.52	2	< 0.025
	10	28	7.32	2	< 0.05
D. merriami	3	20	2.91	2	> 0.1
	10	53	5.97	2	< 0.06
female	10	28	13.5	2	< 0.005
male	10	21	11.6	2	< 0.005
D. microps	3	13	39.83	2	< 0.005
	10	12	22.3	2	< 0.005
INTERSPECIFIC					
merr.-microps	3	20	0.53	2	> 0.1
	10	53	1.23	2	> 0.1
microps-long.	3	13	2.05	2	> 0.1
	10	12	1.85	2	> 0.1
merri.-long.	3	20	5.86	2	< 0.06
	10	53	12.22	2	< 0.005

use of all microhabitats (Chi^2 = 5.46, $p < 0.05$). In 1981 *D. merriami* and *D. microps* deviated significantly from equal use of all habitats (Chi^2 = 4.14, $p < 0.05$, and Chi^2 = 5.40, $p < 0.05$ respectively), with both species of *Dipodomys* favoring the open microhabitat. In 1981 *P. longimembris* did not deviate significantly from equal use of all microhabitats, but, consistent with the 1980 data set, it was caught most often in the bush microhabitat.

Chi^2 contingency tables were used to compare the preferences of species for microhabitats with and without species removals (Tables 2, 3). Intraspecifically, removal of a species produced no significant shifts in the use of microhabitats. Interspecifically, *P. longimembris* had a significant reaction to the removal of *D. merriami* (in 1980 Chi^2 = 5.79, $p < 0.05$, in 1981 Chi^2 = 1.77, $p > 0.10$, combined Chi^2 = 7.21, $p < 0.01$). In both years the use of microhabitats by *P. longimembris* shifted toward the open when *D. merriami* was removed. Removal of *D. microps* did not produce a significant shift in the use of microhabitat by *P. longimembris*. Neither *D. merriami* nor *D. microps* showed a shift in microhabitat use in response to the removal of any species. Detailed information on the estimated number of animals on grids can be found in Lemen and Freeman (1986).

We calculated that the effect of trap competition on the relative availability of traps was small (less than 1%) because the three heteromyids all used the microhabitats in about equal proportions and because we had only moderate trap success (normally 15–20%).

As for the spatial relationships of these rodents, we calculated a center of activity for all individuals on the control grids about three weeks after the initial census. Using this center of activity, we found both intra- and interspecific distances to nearest neighbor. These distances were compared to the expected distributions of distances if we assume a random distribution of the centers of activity (Pielou 1974). The results are shown in Table 4. Both *P. longimembris* and *D. microps* were hyperdispersed intraspecifically. *Dipodomys merriami* was almost significantly hyperdispersed on grid 10 with $p = 0.06$. Interspecifically, *P. longimembris* and *D. merriami* were the only species that were hyperdispersed.

Our analysis of fecal pellets confirms that there are two types of diets in the three heteromyids under study at this site (Lemen and Freeman 1986). *Dipodomys merriami* and *P. longimembris* eat a wide variety of materials including vegetation, seeds, and insects, while *D. microps* concentrates on leaf material.

Discussion

We expected *D. merriami* to prefer the open microhabitat and *P. longimembris* to prefer the bush microhabitat (Rosenzweig and Winakur 1969, Lemen and Rosenzweig 1978, Brown 1975). Based on these expectations, we predicted that removal of *D. merriami* would cause *P. longimembris* to increase its use of the open microhabitat. *Dipodomys merriami*, however, showed only a slight preference for the open, a preference not statistically significant in 1980. This seems to invalidate the basis for the prediction of a shift in foraging by *P. longimembris*. In spite of this, when *D. merriami* was removed, *P. longimembris* shifted its use to the open microhabitat as originally predicted. One explanation for the shift by *P. longimembris* is that *D. merriami* is detecting and forcing the smaller animals out of the open areas more effectively than from the bushes. Removal of *P. longimembris* had no effect on the foraging of *D. merriami*. *Dipodomys merriami* does have a high overlap in diet with *P. longimembris*, and both Price (1978) and Wondolleck (1978) found shifts in the use of microhabitats by *D. merriami* in response to short-term removals of *Perognathus*. Our results, although differing from those of Price (1978) and Wondolleck (1978), are consistent with the idea that the behaviorally dominant species will not adjust its foraging behavior with the short-term removal of subordinate species. Over a longer period of time, as seed densities in microhabitats change, *D. merriami* might alter its selection of microhabitats. The long-term study to demonstrate the effect of removing a small heteromyid on the density or foraging behavior of a larger species has not been done. Long-term studies by Munger and Brown (1981) have documented the effects of removing large species on the remaining smaller species.

The reaction of the other rodents to removal of *D. microps* is a measure of the importance of competition for food in these species. If food is competed for, then the folivorous *D. microps* should not compete strongly with the granivorous *D. merriami* or *P. longimembris*. Removal of *D. microps* should have no effect on microhabitat preferences of *D. merriami* and *P. longimembris*. This prediction is confirmed by our data. Further, the removal of *D. merriami* or *P. longimembris* should have no effect on the habitat preference of *D. microps*. This prediction is also confirmed.

Presence of *D. microps* allows one more comparison. *Dipodomys merriami* and *D. microps* share many morphological characteristics but differ in diet and, by inference, in competition with *Perognathus*. The evolutionary response of *D. merriami* to avoid competition with *P. longimembris* would not be expected in *D. microps*. Our data indicate that *D. merriami* and *D. microps* have similar patterns of microhabitat use. Therefore, we have no evidence that foraging behavior of *D. merriami* has been modified by competition with the other seed-eating rodents.

If the rodents in this community are competing and spacing themselves for minimum overlap, we would expect a hyperdispersion pattern of nearest neighbor distances (O'Farrell 1980, Schroder and Geluso 1975). Intraspecifically, both *P. longimembris* and *D. microps* were hyperdispersed (Table 4). *Dipodomys merriami* did not show a statistically significant pattern of hyperdispersion, but it very nearly did. Interspecifically, *P. longimembris* and *D. merriami* are hyperdispersed, but *D. microps* is randomly distributed with respect to both. These results are consistent with the hypothesis that these rodents are using members of their own species and sometimes members of other species (if there is high overlap in diet) as cues for spatial distribution.

In summary, we have strong evidence that both food and microhabitats are competed for by these heteromyids. We infer the importance of microhabitats based on the reaction of *P. longimembris* to the removal of *D. merriami*. We infer the importance of food based on the lack of response when *D. microps* is removed and based on the pattern of hyperdispersion found between granivores but not between granivores and foliovores. We also have evidence that interference competition, based on a dominance hierarchy, is present. We infer the importance of interference competition based on both the short-term reaction of *P. longimembris* to the removal of *D. merriami* and the failure of *D. merriami* to respond to the removal of *P. longimembris.*

Change in foraging behavior by *P. longimembris* in response to the removal of *D. merriami* is only 8%. This small change is consistent with the small increase in numbers of *P. longimembris* when *D. merriami* is removed (Lemen and Freeman 1986). We found that approximately 13 *D. merriami* have to be removed to expect an increase of 1 *P. longimembris.* We conclude that short-term perturbations do produce evidence of competition for food and microhabitats, but these interactions are weak. It may be that long-term removals, with enough time passing to affect food resources on grids, would show stronger interactions (as found by Munger and Brown 1981 and Brown and Munger 1985), or that short-term perturbations are more important in other years or places (as found in Lemen and Freeman 1983), or that competitive interactions are simply weak in this community. More work will have to be done to resolve this problem.

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SEQUENCE OF EPIPHYSEAL FUSION IN THE ROCKY MOUNTAIN BIGHORN SHEEP

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Abstract.—Sequence and timing of epiphyseal fusion of the postcranial skeleton of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) was examined. Ages up to four years can be determined. Slight differences were found in the time of fusion between males and females. These do not prevent determining the age of a skeleton within a period of two or three months, an accuracy comparable to existing techniques that involve tooth eruption schedules, horn annulations, or incisor cemental annulations.

Several techniques have been developed or proposed on skull or mandible characteristics to determine ages of bighorn sheep (*Ovis canadensis canadensis*). These include tooth eruption schedules (Cowan 1940, Deming 1952, Hemming 1969), cemental annuli accretion rates (Hemming 1969, Turner 1977), horn annulation counts (Cowan 1940, Murie 1944, Taylor 1960, Welles and Welles 1961, Geist 1966, Hemming 1969, Turner 1977), and body weight or other physiologic features (Klein 1964, Hansen 1965, Blood et al. 1970). Taylor (1960) presents a small amount of data on epiphyseal fusion of three selected long bones and the vertebral column. Without skulls or mandibles, only general size difference patterns in skeletal development (an inaccurate method because of the sexual dimorphism seen in adults of this species) can be used to establish age of postcranial skeletal remains of bighorn sheep.

A technique also used to age animals utilizes the sequence of epiphyseal fusion of the postcranial skeleton. This sequence has been documented for *Bison bison* (Duffield 1973), *Odocoileus hemionus* (Lewall and Cowan 1963), *O. virginianus* (Purdue 1983), *Cervus elaphus* (Knight 1966), *Ursus americanus* (Marks and Erickson 1966). Limited data are available for other mammalian species (Todd and Todd 1938, Madsen 1967). The sequence of fusion with advancing age has been well established for most domestic animals, including sheep (Getty 1975). However, except for Taylor's (1960) brief mention, there has not been a complete fusion sequence established as an aging technique for the postcranial skeleton of bighorn sheep similar to those established for other taxa. The present study was undertaken to provide this information on the Rocky Mountain bighorn sheep.

Materials and Methods

Skeletons of 1 fetus, 6 neonates of unknown sex, and 44 older animals (23 females and 21 males, Table 1) were examined. Yearly age classes of these animals were established from tooth eruption schedules (Hemming 1969, Deming 1952). A median birth period of the first week in June was assumed (Thorne et al. 1979, Turner 1977). Month or week of death was determined from mortality data furnished by the Colorado Division of Wildlife or the Wyoming Game and Fish Department. Differences between the two dates provided monthly age classes within the yearly age classes. Except for neonates and the fetus, most specimens used in the study either died in the wild or were live-trapped animals that died in captivity within one year of capture. The remaining animals were in captivity up to three years before their death. Given this source of specimens, any potential bias or early fusion that might have resulted from probably improved nutrition and related body changes of animals pen-reared from birth was greatly reduced.

Because all sheep in this study were born in the wild, no actual age of any specimen is known. However, by combining the information provided by the eruption schedules and

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TABLE 1. Rocky Mountain bighorn sheep specimens examined.

Catalog number[a]	Sex	Age
UWA-8272B	unknown	5-month fetus
UWA-8345B	unknown	newborn
UWA-8346B	unknown	newborn
UWA-8347B	unknown	newborn
UWA-8348B	unknown	newborn
UWA-8349B	unknown	newborn
UWA-8350B	unknown	newborn
UWA-8214B	unknown	one week
UWA-8621B	female	less than 4 months
UWA-8270B	female	less than 4 months
UWA-8353B	female	greater than 4 months
UWA-8359B	male	4 months
UWA-8358B	male	4.5 months
UWA-8623B	female	7.5 months
UWA-8619B	female	7.5 months
UWA-8622B	male	7.5 months
UWA-8211B	male	7.5 to 8 months
UWZ-5394	male	7.5 to 8 months
UWA-8429B	male	8 months
UWA-8430B	male	8 months
UWA-8431B	male	8 months
UWA-8432B	female	8 months
UWA-8433B	female	8 months
UWA-8230B	male	9 months
UWA-8231B	male	9 months
UWA-8354B	female	1 year, 4 months
UWA-8398B	female	1 year, 5 months
UWZ-5395	male	1 year, 5 months
UWA-8355B	female	2 years, 2.5 months
UWA-8357B	male	2 years, 3 months
UWA-8248B	female	2 years, 3.5 months
UWA-8252B	female	2 years, 4 months
UWA-8269B	female	2 years, 5 months
UWA-8397B	male	2 years, 5 months
UWA-8290B	male	2 years, 6 months
UWA-8565B	male	2 years, 7 months
UWA-8435B	male	2 years, 8 months
UWA-8356B	female	3 years, 3 months
UWA-8249B	female	3 years, 4 months
UWA-8333B	female	3 years, 4 months
UWA-8253B	female	3 years, 4 months
UWA-8360B	female	3 years, 4 months
UWA-8415B	male	3 years, 4 months
UWA-8410B	male	3 years, 4 months
UWA-8396B	female	3 years, 5 months
UWA-8204B	female	3 years, 6 months
UWA-8210B	male	3 years, 6 months
UWA-8197B	male	3 years, 6 months
UWA-B0340	male	3 years, 6 months
UWA-8544B	female	3 years, 6 months
UWA-8309B	female	3 years, 8 months

[a] UWA = Univeristy of Wyoming, Anthropology Collections.
UWZ = University of Wyoming, Zoology Museum Collections.

the months of death, I feel ages of the specimens as presented here were adequate for the present purpose. Regional variation was minimized by examination of specimens from the Colorado Front Range and four Wyoming mountain ranges (Medicine Bow Mountains, Big Horn Mountains, Wind River Mountains, and Absaroka Range). Osteological nomenclature and terminology follow Getty (1975).

All bones of each skeleton were examined. The degree of ossification at each location where an epiphysis and a diaphysis occur was recorded. Only those locations where ossification has occurred are discussed in the individual age classes below. If a location is not discussed, it has already fused and therefore is discussed in a young age class, or it fuses at a later time and is discussed in an older age class. Four degrees of ossification were used and are defined as follows:

STAGE 1: Unfused. Epiphysis is completely separate from diaphysis with no ossification between the two portions of bone.

STAGE 2: Beginning to fuse. Ossification has started between epiphysis and diaphysis, but surface of the epiphyseal groove is open.

STAGE 3: Fused but epiphyseal line is visible. Diaphysis and epiphysis are completely joined, but fusion line can still be seen.

STAGE 4: Completely fused. Line of epiphyseal fusion is no longer visible.

FUSION SEQUENCE

Five-month fetus (N = 1): All bones are at fusion stage 1.

Neonates (N = 6): Central and fourth tarsals are at stage 2, forming the centroquartel bone. Distal pubis and ischium are at stage 4, but proximal ends of these bones are still at stage 1. Left and right halves of thoracic neural arches are at stage 3.

One week (N = 1): Centroquartel fusion is now at stage 3. Left and right halves of thoracic neural arches have advanced to stage 4. Cervical, lumbar, and sacral neural arches are at stage 3, except for the odontoid process of the axis (second cervical) which is still at stage 1.

Four month, both sexes (N = 4): All elements of carpus are at fusion stage 4. All tarsus elements except for centroquartel and calcaneal tuber are also at stage 4. Centroquartel is at stage 3 and calcaneal tuber is at stage 1. Centra and neural arches of all vertebrae are now at stage 3. Rib tubercles are at stage 4 fused with ribs. Proximal epiphyses of both metacarpal and metatarsal are at stage 4. Proximal epiphysis of radius is at stage 3.

Four month, male (N = 1): Lateral halves of atlas (first cervical) are at stage 4 on ventral side and stage 1 on dorsal side. Odontoid process of axis is at stage 3. Distal humerus epiphysis is stage 2. The two distal epiphyses of the metatarsal and metacarpal are fused with each other (stage 4) but at stage 1 with diaphyses.

Four and one-half month, male (N = 1): Distal humerus and proximal radius are at stage 4. Fusion between the illium, pubis, and ischium is at stage 4. Supraglenoid tubercle (Tuber scapula) is at stage 4.

Seven and one-half to nine month, male (N = 8): All epiphyses at stage 3 at four months are now at stage 4.

Seven and one-half to eight month, female (N = 4): Proximal epiphysis of second phalange is at stage 4. Centroquartel is still at stage 3. Fusion on dorsal atlas is at stage 3. Odontoid process of axis is stage 4 with the rest of the atlas. Illium is stage 3 with pubis and ischium at the acetabulum. Supraglenoid tubercle is stage 4, as is proximal radius. Distal epiphyses of metacarpals and metatarsals are in stage 4 with each other, but still at stage 1 with diaphyses.

One year, five month, male (N = 1): Fusion sequence on all bones available is the same as seven-and-one-half-month males. Overall size increased during the year's growth. This specimen was lacking the lower extremities, and so the fusion stage of phalanges is unknown.

One year, four to five month, female (N = 2): Proximal end of first phalange is at stage 4. Fusion of the three innominate elements is also at stage 4.

Two year, two and one-half month, female (N = 1): Distal tibia is at stage 2. Second, third, and fourth sacral vertebrae are at stage 2 on their lateral processes, but sacral epiphyses are still at stage 1. Minor trochanter of femur is at stage 1.

Two year, three month, male (N = 1): Proximal end of first phalange is at stage 3. Second, third, and fourth sacral vertebrae are at stage 2 on their lateral processes, but sacral epiphyses are still at stage 1.

Two year, three and one-half month, female (N = 1): All sacral vertebrae are now at stage 4 on lateral processes. Distal tibia, distal metacarpal, and minor trochanter of femur are all at stage 4.

Two year, four to five month, female (N = 2): Anterior epiphysis of first sacral vertebra is now at stage 4 with the vertebra. Other epiphyses on the sacrum are at stage 3. Rib heads are now at stage 2. Distal femur and distal metatarsal are at stage 4. Proximal epiphysis of femur and calcaneal tuber are at stage 3.

Two year, five to eight month, male (N = 4): Distal tibia is at stage 2. Humerus head and major tuberosity are at stage 3 with each other, but at stage 1 with the diaphysis. Femur head is at stage 4 with greater trochanter. Neither is fused to the diaphysis.

Three year, three month, female (N = 1): Rib heads are at stage 4 with the rest of the rib. Proximal femur is still at stage 3. Humerus head and major tuberosity are at stage 3 with each other but at stage 1 with diaphysis.

Three year, four month, both sexes (N = 6): Caudal vertebrae epiphyses are at stage 4. All sacral vertebrae epiphyses are at an advanced stage 3. Anterior and posterior epiphyses of seventh lumbar vertebra are at stage 4, as are anterior epiphyses of fifth and sixth lumbar vertebrae. Proximal and distal femur, proximal tibia, proximal humerus, ulna olecranon process, distal ulna, distal radius, and calcaneal tuber are all at stage 4.

Three year, five to six month, both sexes (N = 6): Anterior epiphyses of cervical vertebrae three through seven are at stage 2. All lumbar vertebrae epiphyses are at stage 4. Thoracic vertebrae epiphyses are at stage 2 (posterior vertebrae more so than anterior). All long bones are now at stage 4.

Three year, eight month, female (N = 1): All postcranial elements of this specimen are at stage 4. The sternebrae have also fused together in this specimen, although other specimens in the collection from older age classes do not have fused sternebrae. This may be irregular in fusion, depending on the individual.

DISCUSSION

The epiphyseal fusion sequence in the postcranial skeleton of the Rocky Mountain bighorn sheep follows the same yearly sequence in the two sexes. During the first year, however, males are slightly ahead of females when specimens of the same age are compared. In succeeding years, fusion in females is slightly ahead of males. This may reflect faster growth rates of males during the first year and quicker maturation of ewes in suc-

TABLE 2. Summary of known stage 4 fusion times, Rocky Mountain bighorn sheep. M = males. F = females.

Element	Neonate	One week	Four to five month	Seven to nine month
First phalanx (proximal)				
Second phalanx (proximal)				F
Metacarpal (proximal)			M-F	
Metacarpal (distal)				
Metacarpal (distal epiphyses)			M	F
Radius (proximal)			M	F
Radius (distal)				
Ulna (proximal)				
Ulna (distal)				
Humerus (proximal)				
Humerus (distal)			M	
Humerus (proximal epiphyses)				
Scapula (supraglenoid process)			M	F
Metatarsal (proximal)			M-F	
Metatarsal (distal)				
Metatarsal (distal epiphyses)			M	F
Tibia (proximal)				
Tibia (distal)				
Femur (minor trochanter)				
Femur (head to greater trochanter)				
Femur (proximal)				
Femur (distal)				
Innominate (distal pubis and ischium)	M-F			
Innominate			M	
Cervical vertebrae (epiphyses)				
Atlas vertebrae (lateral halves)			M	
Axis vertebra (odontoid process)				M-F
Thoracic vertebrae (neural arches)		M-F		
Thoracic vertebrae (epiphyses)				
Lumbar vertebrae (epiphyses)				
Sacral vertebrae				
Sacral vertebrae (anterior epiphyses)				
Sacral vertebrae (lateral processes)				
Vertebrae (centra and neural arches)				M
Rib (tubercles)			M-F	
Rib (head)				
Carpal (all elements)			M-F	
Tarsal (centroquartel)				M
Tarsal (calcaneal tuber)				

ceeding years (Silberberg and Silberberg 1949).

Comparing results of the present study with Taylor's (1960) work shows some inconsistencies with selected bones. All specimens examined by Taylor were mortalities from the National Bison Range, Montana. Although this range is fenced, sheep are not restricted to small pens and live as natural a lifestyle as possible (Taylor 1960). Growth of Taylor's animals would not have been biased by intensive pen rearing and its accompanying different nutrition (McEwan 1968). Neither was sheep growth biased in the present study. Consequently, results of the two studies should be similar.

Taylor (1960, Table XVII) showed the femur is not fused until five years, nine months of age, two and one-half years after the time shown by the present study. Taylor reported the metacarpal to fuse at three years, eight months, which is one and one-half years later than seen here. The thoracic vertebrae fused at four years, nine months, according to Tay-

Table 2 continued.

One year, five month	Two year, three to five month	Two year, five to eight month	Three year, three to six month	Three year, eight month
F				
	M-F			
			M-F	
			M-F	
			M-F	
			M-F	
			M-F	
	F			
			M-F	
	M-F			
	M-F			
		M	F	
				M-F
		F	M	
F				
				M-F
				M-F
			M-F	
				M-F
		F	M	
	F			
			M-F	
			M-F	

lor. This is one year and two months after that found in this study. Fusion times shown by Taylor for cervical and lumbar vertebrae and humerus agree with the present study.

These discrepancies are unexplained. Exact ages of several of Taylor's specimens (including those particular animals apparently causing the above discrepancies) were not known (Taylor 1960). Since this fusion sequence was first established five years ago, additional specimens not used in the original study have been examined. In all cases, I have been able to age these additional specimens using the fusion sequence to an accuracy comparable to tooth eruption sequences, or to known ages. Based on the consistency with which I have been able to crosscheck this sequence, I feel ages of Taylor's specimens were overestimated. Therefore, the fusions in those skeletons would have appeared to occur later than they did.

The present study has demonstrated that the postcranial skeleton of the Rocky Mountain bighorn sheep can be used to determine age. Allowing for minor sexual differences in the fusion rates, an estimated age to within at least two or three months (Table 2) can be provided. Little if any individual variation in the fusion sequence within the age groupings defined in this study was seen. This is at least as accurate as age determination methods based on skull or mandible characteristics. Tooth eruption and replacement schedules can be used to age within four to six months (Cowan 1940, Deming 1952). Cemental annulations are accurate to within a year (and even then the date of death is needed) (Turner 1977). Horn segment counts are also accurate only to within one year (Cowan 1940, Geist 1966).

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PARASITES OF MOTTLED SCULPIN, *COTTUS BAIRDI* GIRARD, FROM FIVE LOCATIONS IN UTAH AND WASATCH COUNTIES, UTAH

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ABSTRACT.—Between 1983 and 1985, 97 mottled sculpin, *Cottus bairdi* Girard, were examined from five collection sites in central Utah for parasites. Eight different species of parasites were observed, representing seven genera of Protozoa (*Plistophora, Myxidium, Myxobolus, Ichthyophthirius, Trichodina, Apiosoma, Eimeria*) and one genus of Nematoda (*Rhabdochona*). The highest number of parasites was found in sculpin from the Provo River near residential areas, while the lowest number was recorded from Hobble Creek, a nearby pristine area. A complete list of parasites for *C. bairdi* with literature citations is presented. Each observed parasite is discussed emphasizing pathogenesis to the host.

During the past three years (1983–1985) we have examined populations of mottled sculpin, *Cottus bairdi*, from central Utah streams for parasites. Ninety-seven mottled sculpin were examined, representing five collection sites found in Utah and Wasatch counties of central Utah. Many studies pertaining to parasites of fishes center on hosts that have major importance to the commercial and sport-fishing industry. Even though nongame fish species represent potential reservoirs for parasites infecting the game fish, few studies have been published on this group. Hoffman (1967) summarized the literature for known species of parasites for the mottled sculpin. Since that date, one article on *C. bairdi* parasites has been published (Muzzall and Sweet 1986, Table 2).

The objectives of this study were (a) to survey *C. bairdi* from four localities in central Utah for parasites, (b) to update the current list of organisms utilizing the mottled sculpin as a host, and (c) to correlate parasite load with the sites selected that were based on impact from human populations.

Numerous surveys of freshwater fish parasites have previously been conducted in many parts of the United States. However, none of them include the mottled sculpin as the primary host, although several species of parasites were reported from *Cottus* spp.

The mottled sculpin has received little attention from parasitologists even though it supports many parasitic groups. Its benthic habit, population densities, water chemistry, and stress may also influence the occurrence of many parasites. These factors appear to make the mottled sculpin an ideal model to monitor water pollution.

MATERIALS AND METHODS

Ninety-seven sculpin (*Cottus bairdi*) were collected from five sites in Utah and Wasatch counties, Utah. Of these, 15 were collected below the state fish traps on the Strawberry River in Wasatch Co., 12 were collected in Hobble Creek in Hobble Creek Canyon, Utah Co., and 70 were taken during two years from two sites in the Provo River near the Brigham Young University campus in Utah Co. The sculpin were collected using electrofishing gear and seines. They were then placed in buckets containing aerated river water and transported to Brigham Young University and kept alive in aquaria until examination. All fish were examined within two days after capture.

Each fish was examined for gross pathology after which blood samples were taken from peripheral circulation, stained, and examined for blood parasites. A gross ectodermal evaluation was followed by gill and fin scrapings that were observed microscopically. Sterile techniques were used on 10 fish to culture kidney macerate on blood agar to determine bacterial infections. The stomach, intestine, liver, gall bladder, and gills were removed and placed with saline in a separate dish for examination at both the gross and microscopic

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TABLE 1. Summary of parasites observed for the mottled sculpin, *Cottus bairdi*, during 1981 and 1982 from central Utah.

Sample location	Year	Nature of habitat	Number of fish examined	Parasites observed		
				Pleistophora sp.	*Myxidium* sp.	*Myxobolus* sp.
Provo River:						
Residential area	1981	Impacted	27	25.9	0	0
Farming area	1981	Impacted (less severe)	10	10.0	0	0
Provo River:						
Residential area	1982	Impacted	33	36.4	36.4	15.2
Hobble Creek (Canyon)	1982	Pristine	12	58.3	16.7	25.0
Strawberry River (Canyon)	1982	Pristine	15	0.0	13.3	26.6

levels. Any abnormal structures in the throat, stomach, liver, kidney, pancreas, and gall bladder were examined at 1,000X magnification. Methyl green-pyronine Y was incorporated as a vital stain to aid in observing protozoan parasites from host fish. Direct fecal smears were obtained from the intestine, and any coccidia found were stored in 2.5% potassium dichromate w/v. Nematodes were stored in 70% ethanol until identified. For identification, nematodes were cleaned and mounted in lactophenol on glass slides. Gill scrapings were stained with Gomori trichrome stain and silver nitrate (5% solution, Klines method). The musculature of the fish was teased apart, and any cysts found were fixed in buffered 3% gluteraldehyde and prepared through standard methods for electron microscopy.

Other parasites were fixed in 10% buffered formalin for future reference. Photographs were taken of fresh material and fixed material with light microscopy and electron microscopy techniques.

RESULTS AND DISCUSSION

A list of the parasites recovered during this study and their prevalence in infected fish is given in Table 1. Eight species of parasites were observed in varying rates of frequency from the examined fish.

The parasites recovered included both protozoan and helminth examples. Of these, *Trichodina*, *Ichthyophthirius*, *Apiosoma*, *Eimeria*, *Myxidium*, *Myxobolus*, and *Plistophora* are common parasites of fish and are considered to have worldwide distributions (Kudo 1966, Hoffman 1967). The life cycles of these protozoa are direct; therefore, increased host density generally leads to an increased prevalence of the parasite. Although no formal host population estimates were made during the two years of the study, the host density seems to be high in one area of the Provo River where 17 sculpins were captured in two five-foot sweeps of the seine. This high density may account for the high prevalence of parasites in the residential area of Provo. The pathogenicity of the observed parasitic protozoa varies from genus to genus and primarily depends on the density of the parasite for each host.

All of the parasites recovered have been recorded previously in *Cottus bairdi* or other *Cottus* species in America with the exception of the *Myxidium* sp. of Kline. This genus was described from material taken in one cottid in China (Bykhovskaya 1962). According to Dogiel (1958), *Myxidium* is endemic to marine sculpin and has been used to study protozoan evolutionary pathways (Reichenback-Kline 1965). Table 2 lists the parasites of *C. bairdi* in North America with literature citations.

The sculpin in all five study areas contained bacteria cysts. Eighty percent of Strawberry River fish had cocci bacteria cysts in viscera and muscle. Ectodermal bacteria cysts occurred on 87.9% of the fish in the Provo River and on 25% of the fish in the Hobble Creek population. The bacterial cultures on blood agar made with host kidney tissue were negative.

Each parasite will be discussed separately with comments pertaining to host-parasite relationship.

Table 1 continued.

with percent infection for sample group					Number parasites observed	Range for parasite infection (%)
Ichthyophthirius multifiliis	*Trichodina* sp.	*Apiosoma* sp.	*Eimeria duszynskii*	*Rhabdochona cotti*		
14.8	0.0	40.0	3.7	62.9	5	14.8–16.9
30.0	55.5	40.7	40.0	80.0	6	10.0–80.0
0.9	0.0	45.5	40.0	42.4	7	0.9–45.5
0.0	0.0	0.0	12.0	58.3	4	12.0–58.3
0.0	0.0	0.0	0.0	0.0	2	13.3–26.6

TABLE 2. Summary of parasite genera currently listed for *Cottus bairdi* and *Cottus* sp. with reference to primary literature source (from Hoffman 1967 to current sources).

Protozoa	Trematoda	Cestoda	Acanthocephata	Nematoda	Arthropoda
Apiosoma[E]	*Bolbophorus*[F]	*Proteocephalus*[D,L]	*Acanthocephalus*[K]	*Camallanus*[D]	*Ergasilus*[F]
Eimeria[C]	*Bucephalus*[F]	*Schistocephalus*[D]	*Echinorhynchus*[A]	*Contracaecum*[D]	
Epistylis[E]	*Crepidostomum*[F]	*Triaenophorus*[I]	*Leptochynchoides*[F]	*Etonema*[B]	
Ichthyophthirius[C]	*Dactylogyrus*[D,H]		*Metechinorhynchus*[D]	*Haplonema*[I]	
Myxidium[G]	*Diplostomum*[D,E]		*Neoechinorhynchus*[D]	*Raphidascaris*[I]	
Myxobolus[D]	*Gyrodactylus*[D]		*Pomphorhynchus*[F]	*Rhabdochona*[D]	
Plistophora[F]	*Neascus*[F]				
Trichodina[D]	*Nezpercella*[J]				
	Phyllodistomum[D]				
	Prohemistomum[F]				
	Rhipicotyle[F]				
	Tetracotyle[D]				

Reference to citation:
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Plistophora: Microsporida

The small microsporidan *Plistophora* was observed in *C. bairdi* from four of the five collection sites. This group of protozoan parasites is characterized by size. Most microsporidan spores, often contained in cysts, average 2–3 μm (Fig. 1). The *Plistophora* cysts were long, eliptical in shape, and oriented laterally in the host. The sporonts contained an average of 16 spores, which is characteristic of this genus (Fig. 2). The *Plistophora* from *C. bairdi* were found in musculature and had no affinity toward any specific location in the body of the host. The pathogenicity of the microsporidans can be quite severe due to their histozoic and coelozoic nature. Muscle deterioration can be observed for infected tissue at the electron microscopy level of magnification (Figs. 3a, 3b).

The myofibrils of the skeletal muscle tissue are broken down near the large intracellular cyst masses (Figs. 3a, 3b). The 16 or more spores within the sporont have typical polar filaments and a single nucleus (Figs. 4a, 4b). *Plistophora* has been reported from sculpins previously (Table 2); however, species designation has not been published to date (Hoffman 1967).

Myxobolus and *Myxidium:* Myxosporida

Myxosporida is the largest protozoan group that infects fish (Kudo 1966). Myxosporidans have a worldwide distribution and are parasitic in all organs of fish. The life cycle begins

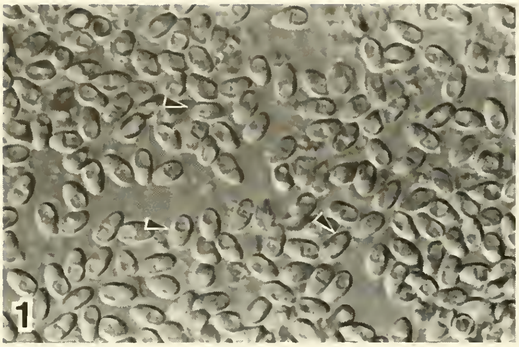


Fig. 1. Mature spores (arrow points) of *Plistophora* from the mottled sculpin, *Cottus bairdi*. Microsporidans are characterized by their size; for *Plistophora* the spores average 2–3 μm in diameter. 1,100X.

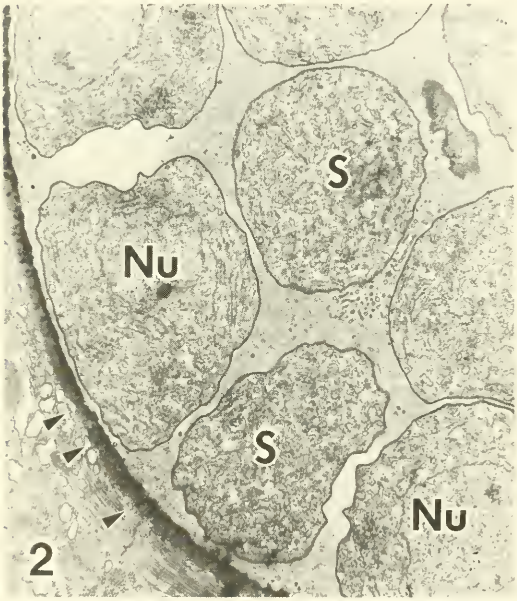
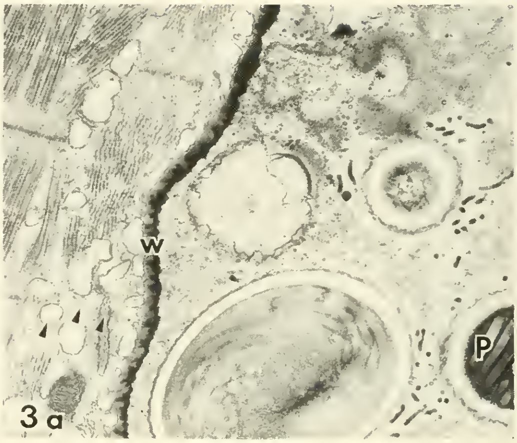
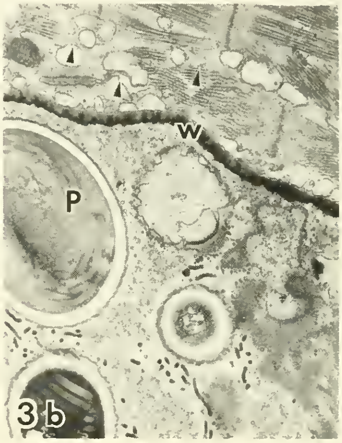


Fig. 2. Transmission electron microscopic micrograph of a sporont (arrow points) with developing spores (S). For *Plistophora* each sporont averages 16 developing spores. Note single nucleus (Nu) within developing spore. 13,800X.



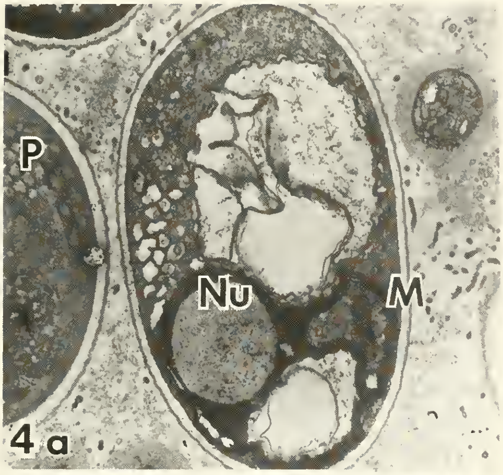


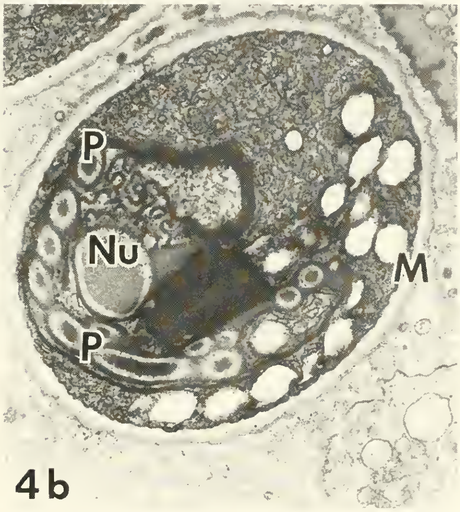
Figs. 3a, 3b. Transmission electron microscopic photomicrograph of a sporont for *Plistophora* found in the musculature of *Cottus bairdi*. Skeletal muscle deterioration is occurring in the host tissue (arrow points). Spore maturity is characterized by the single polar filament (P) forming in the spore. The sporont wall (w) is corrugated and isolated developing spores from host tissue. 13,800X.

with the ingestion of the spores by the host. In the host intestine polar filaments from the spore shoot out from the polar capsules (Reichenback-Kline 1965). Amoeboid embryos (amoebula) emerge and penetrate the intestine and move into organs or muscle tissue where the organism multiplies by plasmotomy. Plasmotomy stages were present in the cysts that accompanied the *Myxidium* spore for the infected gall bladder of mottled sculpin. The observed *Myxobolus* were taken from stomach tissue with the exception of two cysts that were present in the pectoral musculature and a gill arch.

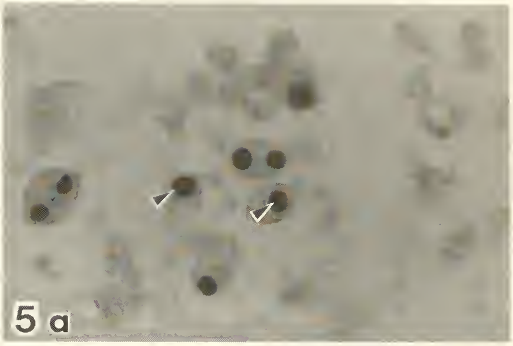
The *Myxidium* spores (Figs. 5a, 5b) are fusiform with two polar capsules. The polar filaments were comparatively long. All spores were found in the gall bladder of mottled sculpin from three collection sites.

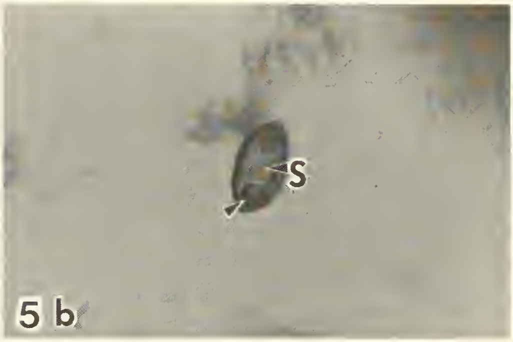
The other myxosporidan, *Myxobolus*, was collected from fish taken from three of the five collection sites. It invades stomach tissue, muscle tissue near the pectoral fin, and muscle tissue near the gill arches. The spores were ovoid in shape with two prominent polar capsules (Figs. 6a, 6b) at the anterior end. The





Figs. 4a, 4b. Mature spores of *Plistophora* infecting the musculature of *Cottus bairdi*. Note the single nucleus (Nu) for each spore, polar filament (P) wrapped around the inside of the multi-layered outer membrane (M). 4a, 13,800X; 4b, 28,000X.





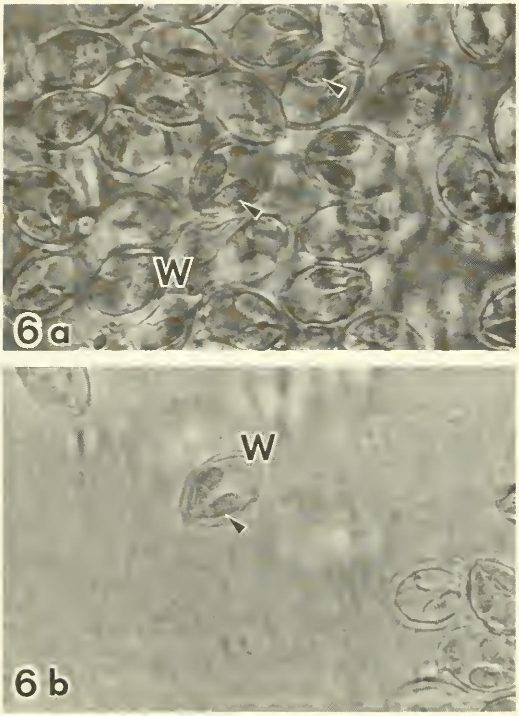
Figs. 5a, 5b. Micrograph of *Myxidium* from the gall bladder of *Cottus bairdi*. A differential stain, Grams stain, was used for Fig. 5a to emphasize the two polar capsules (arrow points) per spore. Fig. 5b is stained with hemotoxylin and eosin, emphasizing the sporoblast (S) inside the spore. 1,100X.

parasite was histozoic in nature occupying muscle tissue (smooth and striated) of the host.

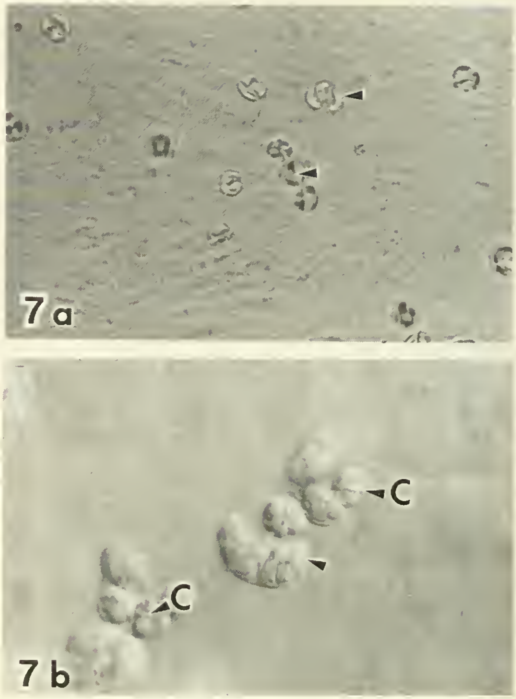
Eimeria: Sporozoa

Freshwater coccidians have been described from Europe, Asia, and North America (Molnar 1973). The genus *Eimeria* is characterized by eight sporozoites within an oocyst. *Eimeria duszynskii* was identified by the presence of crossbanding on the sporozoite end opposite the refractile body (Conder et al. 1980), at 1,000X magnification (Figs. 7a, 7b). This parasite inhabits the epithelium of the intestine and develops through a life cycle of asexual and sexual phases (Hammond 1973). Schizogony is an asexual phase of the trophozoite that encysts in the small intestine. The cyst expels merozoites which differentiate into male and female gametes. In the sexual phase (gametogony) there is a gradual process of invasion into the lining of the intestine (Dogiel 1965). The zygote is passed out in the feces, and, following sporulation, it is taken in by another host. Spores multiply in an asexual phase (sporogony), followed by sporulation in the intestine (Figs. 7a, 7b).

The pathogenicity of coccidians in sculpins has not been described, but in other studies *Eimeria* has been shown to cause mortality in fish (Molnar 1973). The rupture of large numbers of intestinal cells is the chief pathology due to this parasite, and mortality can be associated with decreased ability to absorb nutrients, blood loss, and other physiologic stresses. The damaged tissue can cause physiologic stress and is subject to secondary inva-



Figs. 6a, 6b. The second myxosporidan observed in this study, *Myxobolus*, was found in stomach tissue and in skeletal musculature near the pectoral fin and gill arch. The characteristic spore wall (W) is visible for this sample. Using Nomarsky interference lighting makes the two polar capsules (arrow points) containing polar filaments prominent. 1,100X.



Figs. 7a, 7b. *Eimeria duszynskii* from the intestine of *Cottus bairdi*. The figures represent the sporogonous phase. Spores (arrow points) are released in fecal material whereby other fish can become infected. Note the cross-banding (C) of the sporozoite for Fig. 7b. This is characteristic for the species. 7a, 430X; 7b, 1,100X.

sion by other pathogens.

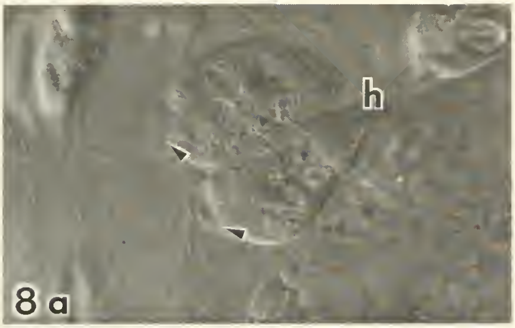
Eimeria was one of the most common parasites observed during this study. It was present in *C. bairdi* from four of the five collection sites. The type species for *E. duszynskii* came from infected fish of the Provo River, one of the sampling sites for this study.

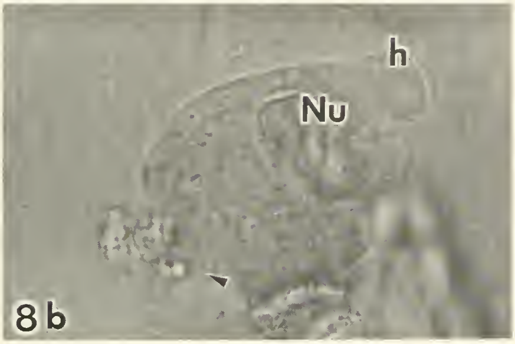
Apiosoma, *Trichodina*, and *Ichthyophthirius:* Ciliata

Apiosoma is a small, staked ciliate that attaches to gill surfaces (Figs. 8a, 8b). This ciliate is 35–44 μm in size and has a characteristic single cone-shaped macronucleus (Hoffman 1970). *Apiosoma* is characterized by a holdfast (scopula) that attaches to the gill surface. There is no documentation to show that this parasite can cause major fish mortality, but the potential exists to kill its host. When present in large numbers, it could tax the respiratory surfaces of the gill lamellae. It was observed in mottled sculpin from the three collection sites on the Provo River. *Apiosoma* numbers fluctuated with seasons, the highest numbers per fish being observed in the spring. Infected gill tissue containing *Apiosoma* was characterized by a fibrous host capsule surrounding the protozoan parasite. There has been only one species described to date infesting fish (Hoffman 1967).

In small numbers *Apiosoma* does not have pathogenicity, but in higher numbers it could create a blockage of the respiratory gill surface. *Apiosoma* was found infesting fish in the same aquatic sites as *Eimeria*.

Trichodina are ubiquitous ciliated protozoan parasites that infest the gill surfaces of fish. The ciliate rarely causes damage to its host. It will rapidly multiply on weakened hosts. It is characterized by three ciliary girdles (aboral) with taxonomically important, radially arranged hooked teeth or denticles (Fig. 9). There are many undescribed species in North American freshwater fishes (Hoffman 1967). For this study, mottled sculpin





Figs. 8a, 8b. The stalked ciliate, *Apiosoma*, which infests the gill surface of *Cottus bairdi*. Note the cilia (arrow points), macronucleus (Nu), holdfast (h) for host attachment, and large size (35–44 μm in diameter). 8a, 430X; 8b, 1,100X. Nomarsky phase interference microscope lighting was used for this figure.

from a single site on the Provo River were infested with *Trichodina* (Table 1).

Trichodina has been associated with mortality where the level of infection is high and abrasion of the gill tissue is too severe for repair. This causes a physiologic stress on the animal, in addition to opening the area for secondary infections. In one instance, *Trichodina* sp. had a significant association with *Gyrodactylus* sp. (Noble 1961).

Ichthyophthirius multifiliis was recovered in gill material of *C. bairdi* taken from all three collection sites on the Provo River. This parasite is very common in freshwater fish and has a worldwide distribution. It has also been the cause of major catfish mortality (Hines and Spira 1973), and much research has been conducted to manage the disease (Farley and Heckmann 1980). This ciliate is one of the largest protozoan parasites for fish. During the trophozoite phase of its life history it can measure up to 1 mm in size and thus the name "white spot disease." It has a characteristic horseshoe-shaped macronucleus that is visible with limited magnification (Figs. 10a, 10b) (McCallum 1982). *Ichthyophthirius* in high numbers is detrimental since it can cover the gill respiratory surface. Agglomerate and benthic life stages are followed by an adult ectodermal phase (Farley and Heckmann 1980). In this stage *I. multifiliis* can burrow under the epithelium of its host, subjecting the fish to potential secondary infections.

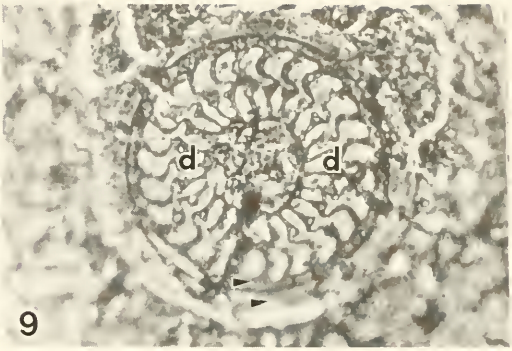


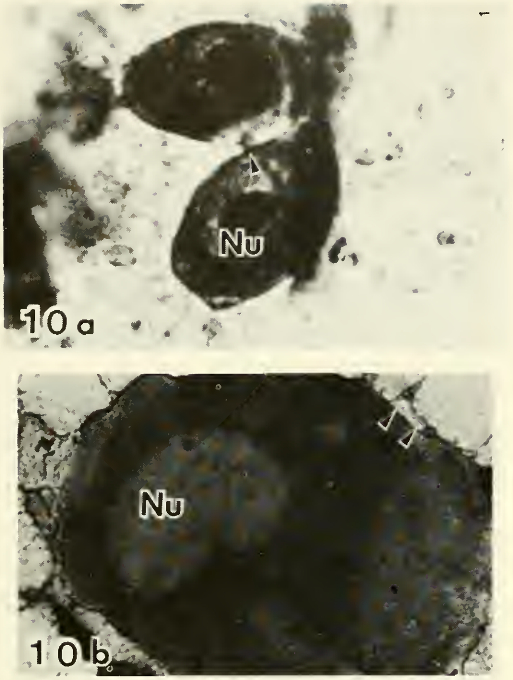
Fig. 9. *Trichodina*, a ciliated protozoan, from infested *Cottus bairdi* gills. Kliens silver stain method was used for emphasis of ciliary rows (arrow points) and denticles (d). Both characteristics are used to taxonomically describe species of *Trichodina*. 1,100X.

The rapid multiplication of *Ichthyophthirius* is one reason it is so pathogenic (Hoffman 1967). The greatest mortality caused by this parasite was reported for channel catfish (*Ictalurus* sp.) (Hines and Spira 1973).

Rhabdochona: Nematoda

Rhabdochona is the only helminth from sculpin found during this survey. Several species of fish are parasitized by this genus of nematodes (Yamaguti 1961). *Rhabdochona cotti* was found in *C. bairdi* at four of the five collection sites. Larval development for *Rhabdochona* occurs in several species of mayfly nymphs (e.g., *Hexagenia*) (Gustafson 1941), thus the ready availability of the nematode for mottled sculpin. Not much is known concerning the pathogenicity of this parasite. A high percentage of infections by acanthocephalan parasites, another helminth, have been reported from winter collections in other surveys of sculpins (Amin and Burrows 1977), but the reason for the high rate of infection by *R. cotti* in the winter-spring season in this study is unknown.

Adult *Rhabdochona* inhabit the intestine of fish. Sections were taken of infected intestine



Figs. 10a, 10b. *Ichthyophthirius multifiliis* that infested the gill surface of *Cottus bairdi* from the Provo River, Utah. Note the large size of the ciliate, the horseshoe-shaped macronucleus (Nu) and the cilia (arrow points). 10a, 100X; 10b, 430X.

containing this parasite and stained using a pentachrome stain (Fig. 11). It is suspected that this nematode has little pathogenicity; but in large numbers the potential for significant intestinal damage exists. The adult nematode has a characteristic buccal capsule with longitudinal ribs terminating anteriorly in pointed teeth (Fig. 11) (Hoffman 1967).

This study has complemented the known parasitofauna of *Cottus bairdi* with the addition of two protozoan species to the current list of 37 parasites (Table 2). There was a paucity of helminth parasites in the examined sculpin which were common for other collection sites (Heckmann 1983).

Ecological Comments

The greatest density of parasites observed, the highest number of species found, and the total number of parasites per fish came from *C. bairdi* inhabiting the Provo River near Brigham Young University (Table 1). This area receives heavy impact from the local human population. In a pristine mountain stream, Hobble Creek, only two species of myxosporidan parasites were observed in 13 and 26% of the examined fish (Table 1).

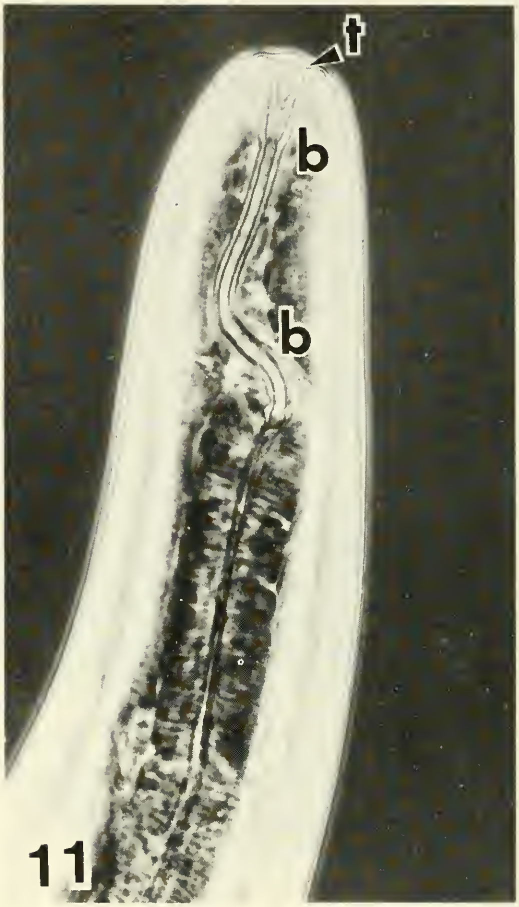


Fig. 11. *Rhabdochona cotti* was the only helminth observed during this study. This nematode was found in the intestine of *Cottus bairdi* and is characterized by a narrow buccal capsule (b) terminating anteriorly in pointed teeth (t). 100X.

ACKNOWLEDGMENTS

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EFFECTS OF ARTIFICIAL SHADING ON DISTRIBUTION AND ABUNDANCE OF JUVENILE CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)

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ABSTRACT.—The influence of artificial shade on the distribution and abundance of juvenile chinook salmon was studied in a side channel of the South Fork Salmon River, Idaho. Fish biomass and abundance were greater in shaded than in unshaded areas when compared to both cumulative incident light reaching the study sections during the 72-hour test runs and instantaneous incident light conditions at the end of the 72-hour test runs. Because conditions may be atypical at the time of instantaneous light measurement, we prefer cumulative incident light for relating light and shade conditions to daytime distribution (abundance and biomass) of juvenile chinook salmon.

Cover is one of the most important habitat components for anadromous salmonids during the freshwater-rearing phase of their life cycle. Cover can be described either as submerged cover or overhead cover (Reiser and Bjornn 1979). Examples of submerged cover are rocks and boulders, large organic debris, and aquatic vegetation. Overhead cover includes riparian vegetation, water turbulence, logs and other debris on or close to the water surface, and overhanging or undercut banks.

Many of these cover types can also be classed as cover with form; for example, rocks, large organic debris, and undercut banks (Brusven et al. 1986). Riparian vegetation can be classified as either cover with form or cover without form. Cover without form provides shade or insulation against temperature extremes. Shade may be important in maintaining cool water; it may also provide protection for fish from predators.

Several studies have demonstrated the use of shade by salmonids where the cover is on or below the water surface. In a shallow (24–29 cm) tank, small brook trout (*Salvelinus fontinalis* [Mitchill]) preferred shade as did Atlantic salmon (*Salmo salar* Linnaeus) parr when they were the only species present; in the presence of trout, salmon parr were generally found in unshaded areas (Gibson and Power 1975). Gibson and Power (1975) found that in a deep tank (43–50 cm) neither species preferred shade. Rainbow trout (*Salmo gairdneri* Richardson) fry showed no apparent preference for overhead cover in an artificial tank, but yearlings preferred the covered portion of the tank at all light intensities, except when the yearlings were randomly distributed in total darkness (McCrimmon and Kwain 1966). Juvenile Atlantic salmon were negatively phototactic at all but the very lowest light intensities (Pinhorn and Andrews 1963, Gibson and Keenleyside 1966). Gibson and Keenleyside (1966) showed that at all light intensities brook trout in laboratory aquaria generally positioned themselves in the dark areas at edges of shadows created by overhead cover. Butler and Hawthorne (1968) found a direct relation between amount of shade provided by overhead cover and its use by rainbow trout, brown trout (*Salmo trutta* Linnaeus), and brook trout. Hoar et al. (1957) found that, when given a choice between light and dark areas, schools of chum salmon (*Oncorhynchus keta* [Walbaum]) or pink salmon (*O. gorbuscha* [Walbaum]) fry remained in the light, and sockeye salmon (*O. nerka* [Walbaum]) fry preferred the dark; coho salmon (*O. kisutch* [Walbaum]) fry showed no preference between light and dark areas. Sockeye and coho smolts stayed in the dark more than did sockeye and coho underyearlings.

Other studies suggested that cover with form plays a much more important role than does shade. DeVore and White (1978) found no significant difference in response between brown trout in different intensities of incident light due to canopy shading; they found, however, a significant difference in response to physical cover with the highest correlation occurring when the cover was closest to the substrate (provided fish could still get under it). Gibson (1978) observed that shade was attractive to both Atlantic salmon parr and brook trout in shallow water; but given the choice of a shallow (30-cm) tank with shade or a deeper (50-cm) tank with no shade, the majority of both species selected the deeper tank. In this study Gibson noted that a turbulent water surface was more attractive to salmon parr than was shade.

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The studies cited above were conducted for the most part in laboratory tanks or aquaria. In natural stream conditions, Gibson (1966) found that brook trout generally remained under overhanging cover, such as alder bushes, except at times of low illumination in early morning and in the evening. He noted that Atlantic salmon parr usually were observed away from such cover; they fed all day in brightly lit open areas of the stream. No significant difference was found between distributions on cloudy and on sunny days for either trout or salmon. When artificial shade was installed along a previously unshaded stream reach, brook trout were attracted to the shaded area (Gibson 1966). In a field study of simulated undercut banks, Brusven et al. (1986) found that 85% of the juvenile chinook salmon (*O. tshawytscha* [Walbaum]) biomass occurred in covered sections of a stream channel.

Hawkins et al. (1983) reported a positive correlation between abundance of salmonids and abundance of invertebrates in several streams in Oregon and northern California. In general they found an inverse relation between shade and density of invertebrates (hence salmonids). Use of specific types of shade cover by salmonids within study reaches was not studied, however.

In a study of temperature selection by young brook trout, Sullivan and Fisher (1954) found that at low light intensities trout responded to temperature without regard to shade, but at high light intensities the trout were not observed in the illuminated part of the laboratory trough—that is, shade was sought in preference to temperature.

The purpose of our study was to evaluate the role of artificial shade on the distribution, abundance, and biomass of juvenile chinook salmon in a flow-regulated channel.

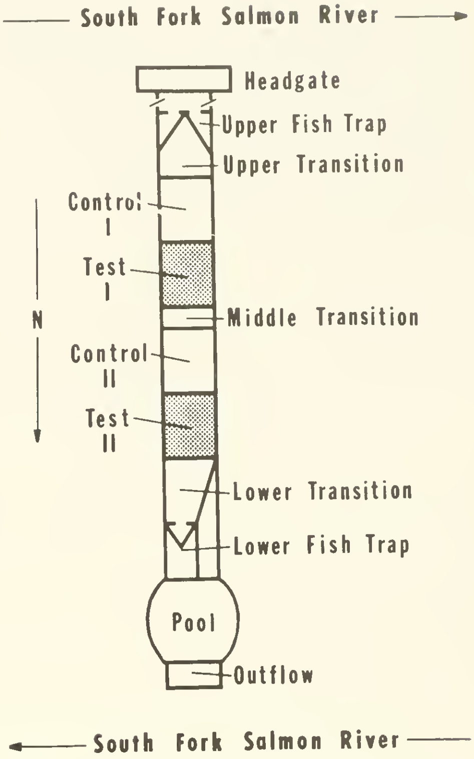

Fig. 1. Study sections of artificial stream channel, South Fork Salmon River, Idaho.

STUDY AREA

The study was conducted in 1977 and 1978 in an abandoned spawning and rearing channel in the South Fork Salmon River drainage in west central Idaho, about 50 km east of Cascade. The channel was constructed over 20 years ago by cutting across an oxbow in the South Fork Salmon River. Since then, the banks have been stabilized by indigenous vegetation. The channel is 160 m long and drops 0.58 m over its length. It has an upper channel (110 m long) and a lower pool (50 m long) (Fig. 1). The substrate is primarily sand (< 1.5 mm) and pebbles (1.0–3.0 cm). A steel headgate controls flow into the channel. The lower 48 m of the channel (exclusive of the pool) was used to investigate fish distribution in relation to simulated shade-producing riparian vegetation.

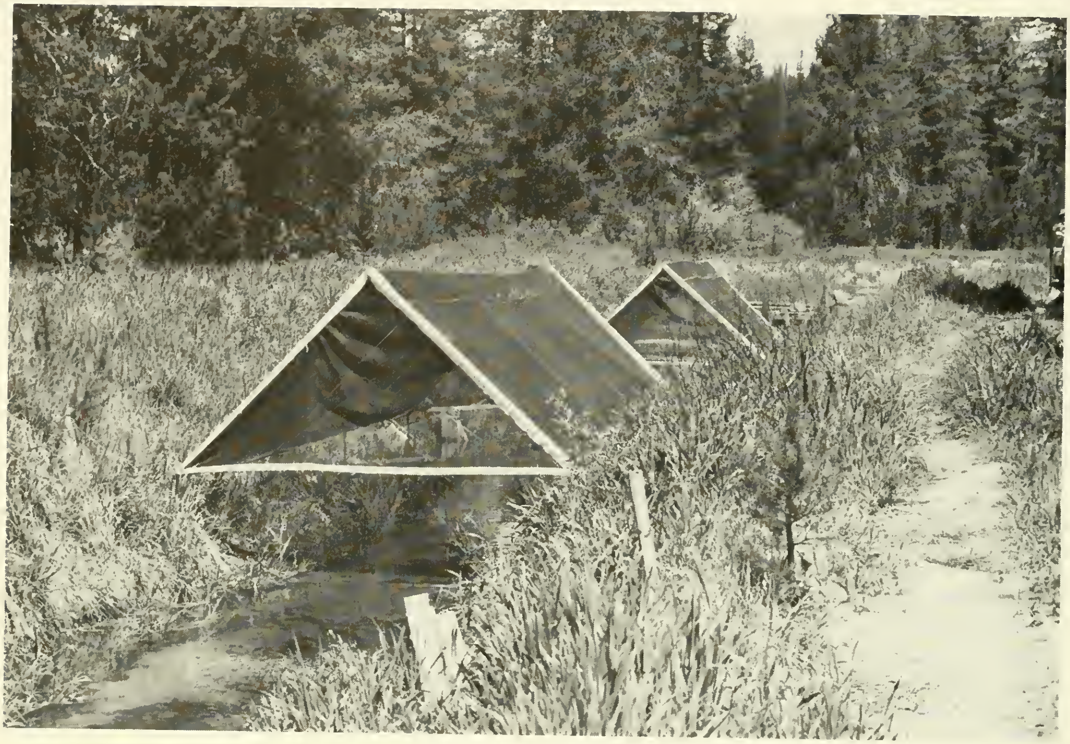

Fig. 2. Shade canopy in treatment section.

The banks of the channel were trimmed to remove rooted aquatic plants, to minimize shading from riparian grasses, and to create a homogeneous habitat throughout the channel. Lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and willows (*Salix* spp.) are sparsely represented on the oxbow. During midday, shading from these plants is minimal; during early morning and late afternoon, however, some shading is apparent on the channel.

Summer-run chinook salmon spawn near the channel, and juveniles use the channel as a rearing area during most years. Steelhead trout (*Salmo gairdneri* Richardson), bull trout (*Salvelinus confluentus* Suckley), mountain whitefish (*Prosopium williamsoni* Girard), and sculpins (*Cottus* spp.) are also found in the main river and occasionally in the channel.

Fish traps were installed at the upper and lower ends of the study reach to determine fish outmigration. Two test units were created within the study reach; each test unit had a treatment section and a control section. Each section was about 7.6 m long and 2.4 m wide; water depth averaged 35–40 cm. Test units and sections within each test unit were also separated by imbedded sills fitted with recessed fish netting. The paired test units were further separated by a 2.8-m transition area to remove the shading effects of a canopy installed over the upstream treatment section.

MATERIALS AND METHODS

SOLAR RADIATION.—To test shade as a factor influencing distribution and abundance of fish, two A-frames were constructed of 19-mm I.D. pipe. They were 7.6 m long, 3.1 m wide at the bottom, and 2.5 m high at the center. In 1977 dark green saran screen[4,5] (20 meshes per 2.5 cm) was placed over the frames in the two treatment sections to form shading canopies (Fig. 2). The control sections were without artificial shade. Light transmittance through a single layer of the screen was 47% when the

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[4] Chicopee Manufacturing Company, Lumite saran screen, fabric no. 50038–00.

[5] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture or the Forest Service of any product or service to the exclusion of others that may be suitable.

TABLE 1. Water temperature (C) measured at end of each test run in 1977 and 1978, SFSR channel.

Test date	Run	Test sections[1] 1T	2T	1C	2C
		°C			
June 1977	1	12.47	12.41	12.48	12.51
	2	14.71	14.64	14.84	14.79
August 1977	1	13.32	13.26	13.38	13.30
	2	13.56	13.60	13.57	13.58
	3 (shade removed)	12.41	12.44	12.43	12.43
July 1978	1	10.56	10.70	10.62	10.61
	2	12.28	12.34	12.41	12.39
August 1978	1	10.00	9.92	10.08	10.11
	2	9.17	9.19	9.21	9.18
	3 (shade removed)	10.21	10.22	10.34	10.22

[1] Sections 1T and 2T are shaded except when otherwise indicated, sections 1C and 2C are unshaded.

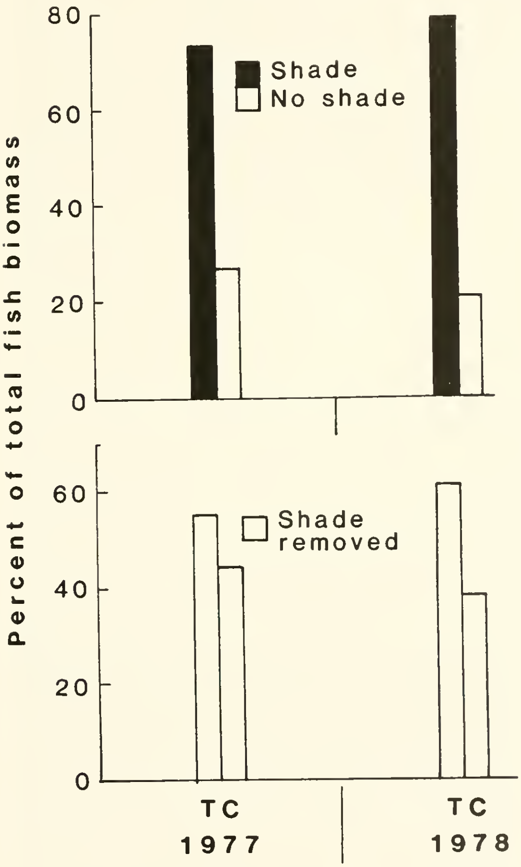

Fig. 3. Fish biomass in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

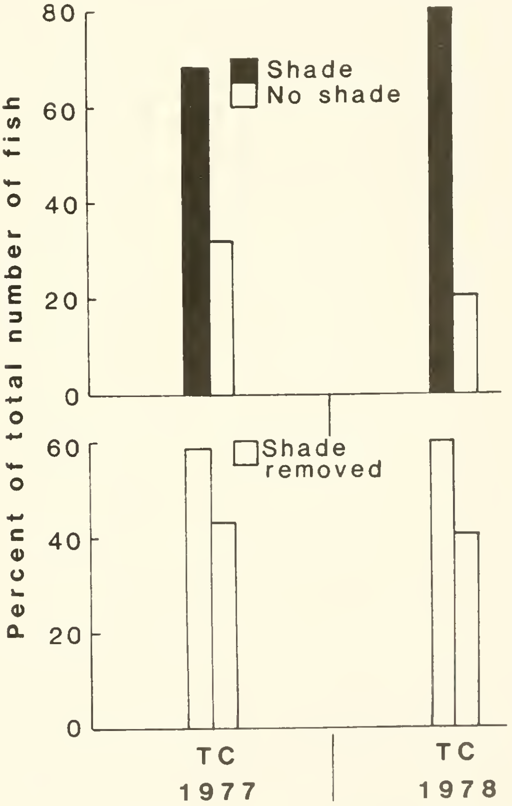

Fig. 4. Fish abundance in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

sun was perpendicular to the material, as determined by a hand-held solarimeter.[6] Sunlight transmittance under semishade among conifers and hardwoods near the channel was 15–55%. Thus, the artificial canopy was similar to the sparse natural canopy of the area. In 1978 darker shade was tested by doubling the screen and rotating the second layer 45 de-

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[6] Matrix Inc., Mark VI Sol-a-meter.

TABLE 2. Cumulative incident light (g cal/cm^2) measured during test runs in 1977 and 1978, SFSR channel.

		Test sections[1]			
Test date	Run	1T	2T	1C	2C
		g cal/cm^2			
June 1977	1	221	187	509	509
	2	635	574	1532	1446
August 1977	1	448	433	1006	1159
	2	484	517	936	1213
	3 (shade removed)	714	788	832	832
Mean[2]		447.0	427.8	995.8	1081.8
		($\bar{X}T = 437.4$)		($\bar{X}C = 1038.8$)	
July 1978	1	225	196	1152	1114
	2	343	296	1710	1694
August 1978	1	182	171	960	1084
	2	188	205	1120	1209
	3 (shade removed)	1028	1007	1115	1210
Mean[2]		234.5	217.0	1235.5	1275.3
		($\bar{X}T = 225.8$)		($\bar{X}C = 1255.4$)	

[1] Sections 1T and 2T are shaded except when otherwise indicated; sections 1C and 2C are unshaded.
[2] Mean for runs with shade in place.

TABLE 3. Incident light (g cal/cm^2 per min) recorded at time of fish capture in 1977 and 1978, SFSR channel.

		Test sections[1]			
Test date	Run	1T	2T	1C	2C
		g cal/cm^2 per min			
June 1977	1	0.5	0.5	1.0	1.0
	2	0.5	0.5	1.0	1.0
August 1977	1	0.4	0.5	0.9	1.0
	2	0.1	0.1	0.2	0.2
	3 (shade removed)	0.7	0.6	0.8	0.8
Mean[2]		0.38	0.40	0.78	0.80
		($\bar{X}T = 0.39$)		($\bar{X}C = 0.79$)	
July 1978	1	0.2	0.3	1.1	1.1
	2	0.2	0.3	1.1	1.1
August 1978	1	0.2	0.2	1.0	1.0
	2	0.2	0.2	0.5	0.8
	3 (shade removed)	0.7	0.7	0.8	0.8
Mean[2]		0.20	0.25	0.93	1.00
		($\bar{X}T = 0.23$)		($\bar{X}C = 0.96$)	

[1] Sections 1T and 2T are shaded except when otherwise indicated, sections 1C and 2C are unshaded.
[2] Mean for measurements with shade in place.

grees over the mesh alignment of the earlier screen, producing 75% shade—more typical of a dense, natural canopy.

Four recording pyranographs[7] measured solar radiation along the four treatment and control sections of the channel during the tests. These were mounted at about the center of each section on 1-m-high stands above the substrate. Incident light intensity in gram calories per square centimeter per minute was read off a pyranograph chart when a test run was completed. The cumulative incident light during a 72-hour test run, in gram calories per square centimeter, was determined by reading the incident light off the pyranograph chart at 2-hour intervals, multiplying each of these readings by 120 (minutes per interval), and summing the 36 observations.

STREAM FLOW.—Water flow through the artificial channel was maintained at approximately 0.11 m^3/s (3.9 cfs) during the tests by an adjustable head gate at the upper end of the channel.

WATER TEMPERATURE.—Water temperatures were measured and recorded in each test section simultaneously by Peabody Ryan Model G-45 recording thermographs.

FISH POPULATIONS.—Juvenile chinook salmon were captured with a 12-volt direct-current backpack electroshocker and a seine

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[7] Weather Measure Corporation mechanical pyranograph, model R401-S.

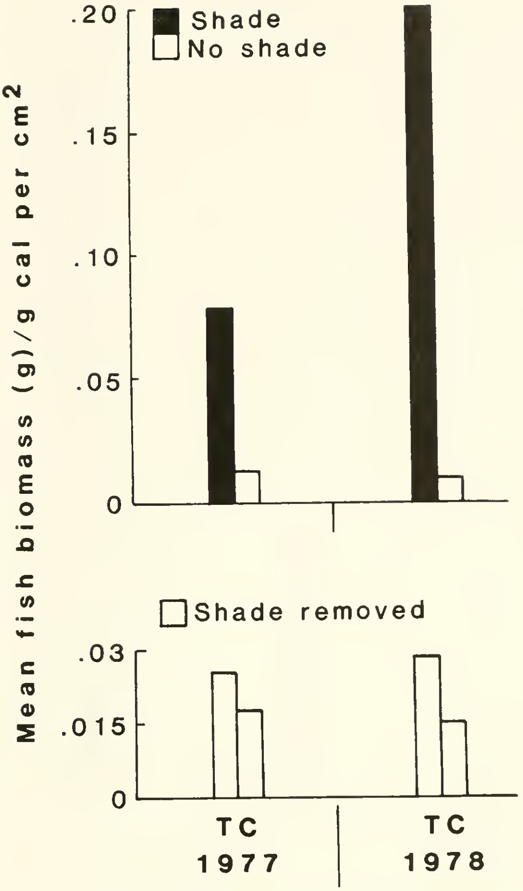

Fig. 5. Ratio of fish biomass to cumulative incident light in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

from the main South Fork Salmon River in the immediate vicinity of the artificial channel. All captured fish were mixed together. Before each test run, all fish were removed from the study reach by electrofishing. Test fish were then added to the study reach until the carrying capacity was established; the carrying capacity was determined by allowing surplus numbers of fish to migrate from the channel. The duration of a test was 72 hours that commenced and ended between 1030 and 1200. This length of time allowed the fish to acclimate and select preferred habitat. After 72 hours elapsed, a series of block nets were pulled simultaneously to isolate each of the four test sections.

After the block nets were in place, fish were removed from each test section, measured (fork length in mm), and weighed to the nearest 0.1 g. After processing, all test fish were released into the main South Fork Salmon River below the artificial channel.

SCHEDULE OF TESTS AND DATA ANALYSIS.—During 1977 and 1978, tests were conducted in late June to early July and again in mid to late August. Two tests were run during each of the two test periods each year. The first test used shade canopies over the treatment sec-

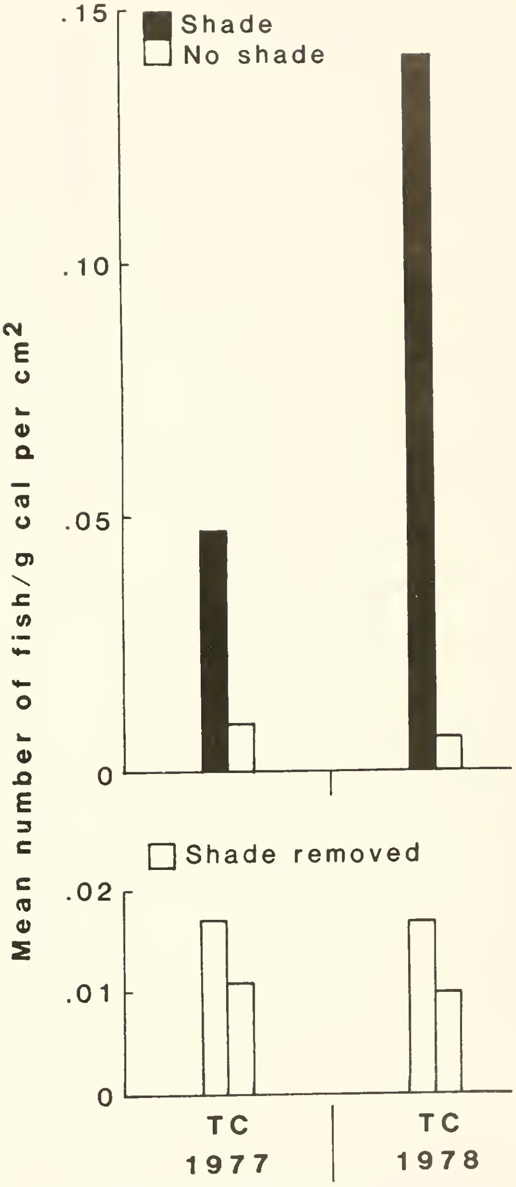

Fig. 6. Ratio of fish abundance to cumulative incident light in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

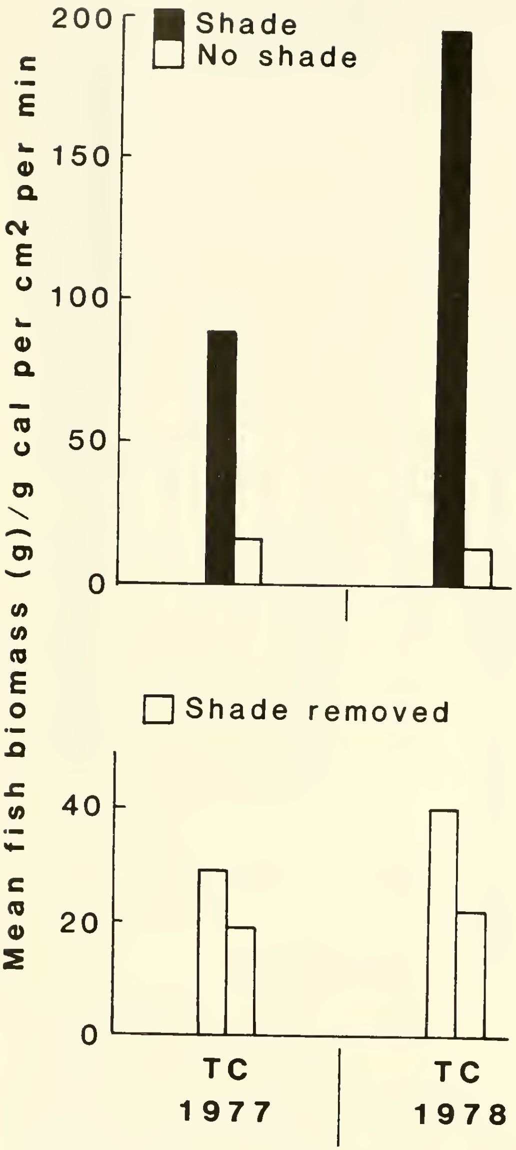

Fig. 7. Ratio of fish biomass to incident light in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

tions. In the second test, shade canopies were removed from the treatment sections to establish fish distribution in the channel without regard to shade.

RESULTS AND DISCUSSION

Because water temperature was essentially the same in each test section (Table 1), choice of section by fish can be attributed to shade.

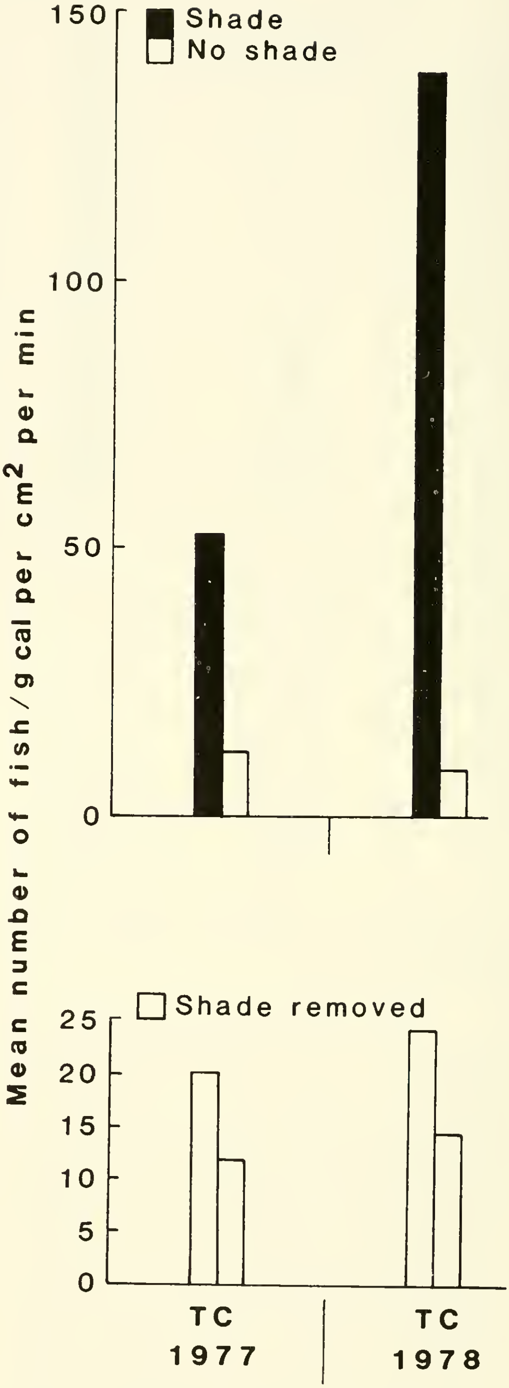

Fig. 8. Ratio of fish abundance to incident light in shaded (T) and unshaded (C) test sections of study channel, 1977 and 1978.

Fish biomass and abundance were greater in shaded than in unshaded areas when the re-

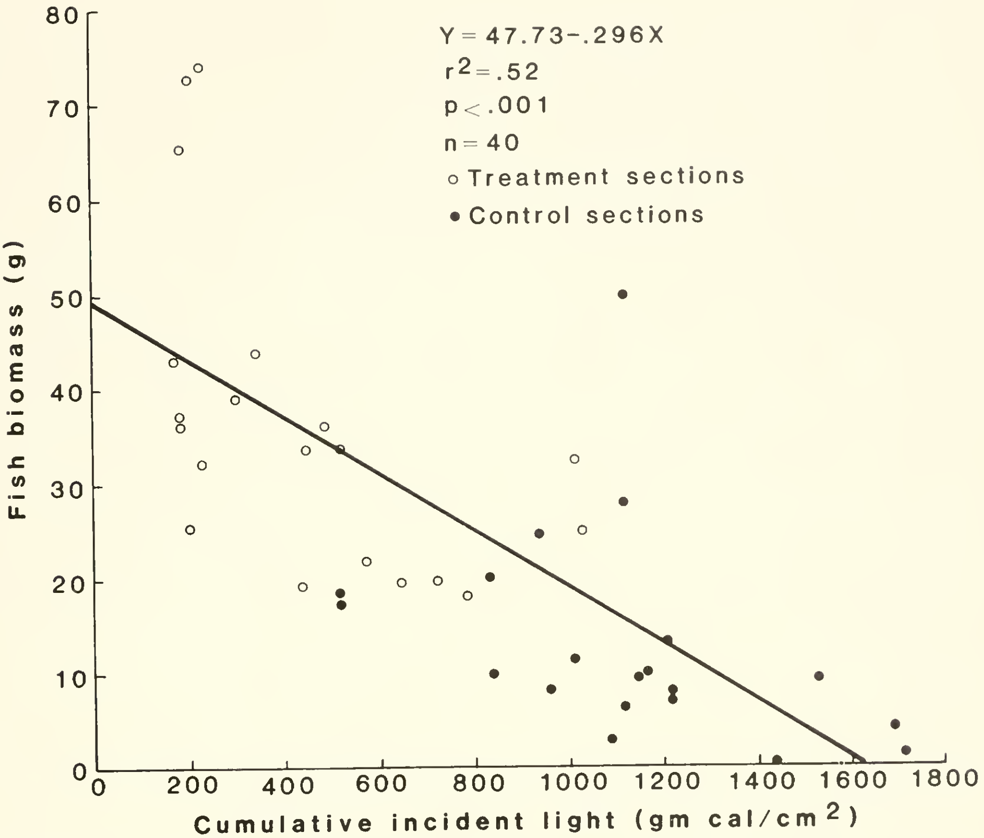

Fig. 9. Relation between cumulative incident light and fish biomass for all test runs, 1977 and 1978 combined.

sults of the June–August tests were pooled for 1977 and 1978 (Figs. 3, 4). Differences between years in fish response to shade were evident, particularly when tests of the shade–no shade choice were compared to tests of shade removal. These differences between years are less apparent when fish biomass and abundance are compared to cumulative incident light during the test runs (Table 2, Figs. 5, 6) and to incident light when the fish were captured (Table 3, Figs. 7, 8).

The only physical variable altered between the two years was the light transmittance of the saran screening. During the 1978 test, 75% shade was achieved, and 47% shade was maintained during the 1977 tests. The cumulative incident light and incident light values during the tests were about two times greater in the unshaded sections than in the shaded sections in 1977 and about four times greater in the unshaded sections than in the shaded sections in 1978 (Tables 2, 3). This corresponds to the difference in light transmittance through the screening between the two years. Although Hoar et al. (1957) determined that juvenile salmon were less photonegative than older fish, the relative age structure of the juvenile salmon used in our study was comparable between the two years and cannot be construed as an explanation of differences between years. The intensity of light, as measured by the pyranographs, was about 20% higher in 1978 than in 1977 (Tables 2, 3). If fish were negatively phototactic, we can hypothesize that the differences in abundance and possibly biomass between shaded and unshaded sections should have been even greater in 1978 than in 1977. This hypothesis was not clearly substantiated when the results for the percentage of fish biomass and abundance were evaluated without regard to incident and cumulative incident light (Figs. 3, 4). We can, however, infer that the hypothesis was substantiated when fish biomass and

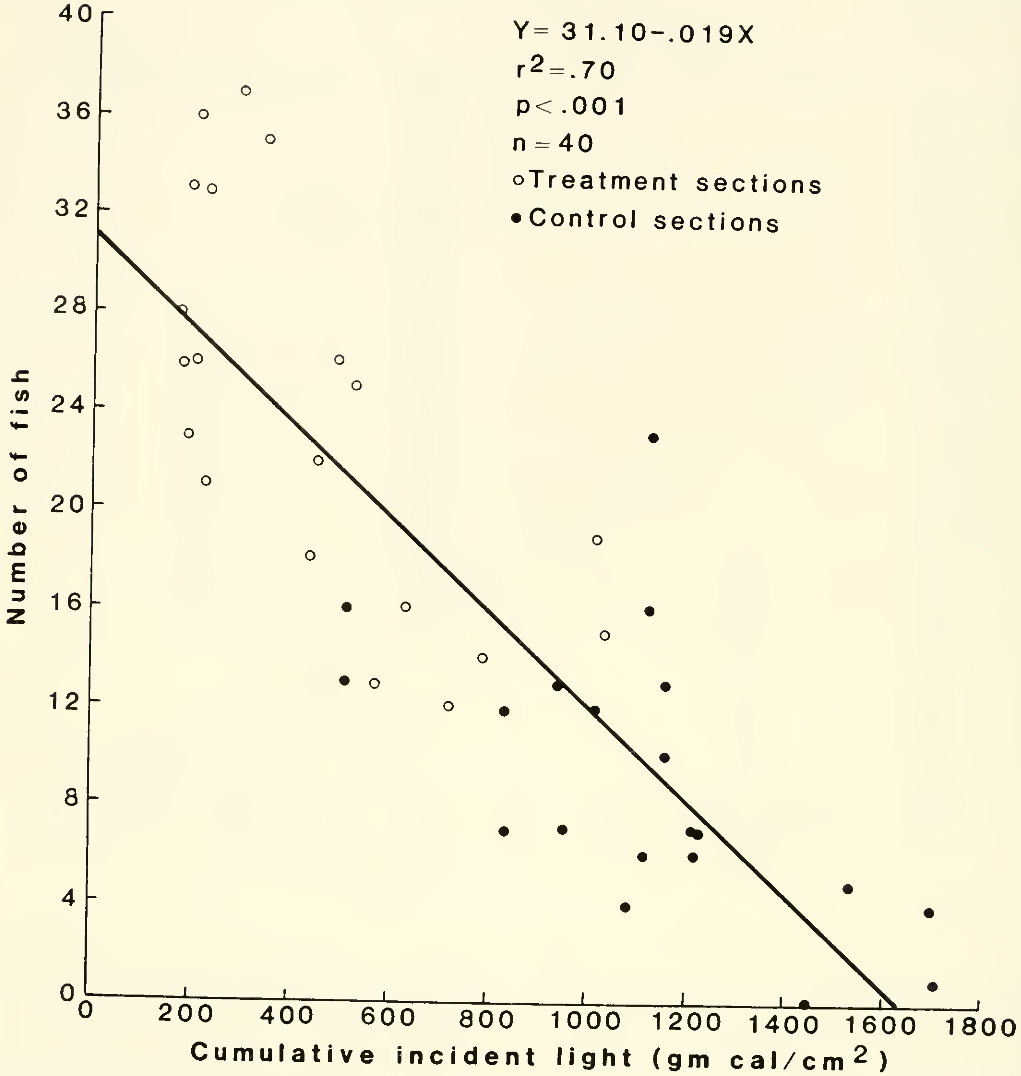

Fig. 10. Relation between cumulative incident light and fish abundance for all test runs, 1977 and 1978 combined.

abundance in relation to cumulative incident light (Figs. 5, 6) and to instantaneous incident light (Figs. 7, 8) were compared between the two years. The hypothesis was further substantiated when data from all tests for both years were combined; highly significant correlations were found between cumulative incident light and fish biomass and abundance (Figs. 9, 10). Chapman and Knudsen (1980) and Hawkins et al. (1983) report that reduced cover supports higher standing crops of salmonids in western streams. Although this is generally true, the studies cited earlier (for example, Gibson and Keenleyside 1966, Butler and Hawthorne 1968) have fairly well demonstrated that most salmonids seek shade cover, particularly at high light intensities. Standing crops may therefore be greater in unshaded stream reaches, but within those reaches, the fish probably seek out shaded habitats. We frequently observed fish maintaining position in the shade provided by the screen covers, but darting momentarily into the unshaded area to secure food and then returning to the shade.

Our results strongly suggest that shade is an important feature of stream habitat and influences the daytime distribution, abundance, and biomass of juvenile salmonids. Under the conditions of cover without form that we simulated and that occur naturally, shade may be a relatively more important feature than in habitats having cover with form, such as overhanging banks, logs, and other debris on or directly over the stream surface. These latter types of cover cast a shade mosaic on the stream surface and substrate that not only changes constantly with the changing angle of the sun but also affects a much smaller area than would general shade provided by a dense canopy of riparian vegetation.

The effectiveness and importance of shade as a cover feature for salmonids likely vary with fish species, age, and the species (or predator-prey) mix. We suggest that measuring cumulative incident light may be important in explaining the daytime distribution, abundance, and biomass of fishes that display strong territorial behavior, such as some salmonids. Validating this hypothesis is an area for future investigation.

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DROSOPHILA PSEUDOOBSCURA (DIPTERA: DROSOPHILIDAE) OF THE GREAT BASIN IV: A RELEASE EXPERIMENT AT BRYCE CANYON

Monte E. Turner[1]

ABSTRACT.—Some populations of *Drosophila pseudoobscura* in the Great Basin have very little genetic variation for third chromosome inversion gene arrangements. These populations are essentially monomorphic for the Arrowhead gene arrangement. At Bryce Canyon, Utah, individuals with other gene arrangements (Standard, Pikes Peak, and Treeline) were released and their frequencies monitored. One generation after release, the released arrangements had increased in frequency from 0.7% to almost 10%. After overwintering, the arrangement frequencies were not statistically different from the prerelease samples. The samples did demonstrate a low-level retention of the released Pikes Peak arrangement. The decline in the released arrangements was probably the result of large population size at Bryce Canyon and the bottleneck effects of overwintering. The results do not seem consistent with a model of the released arrangements having a lowered fitness.a

Natural populations of *Drosophila pseudoobscura* have been studied for over 40 years. Populations were originally cytologically characterized for the gene arrangements of the third chromosome (Dobzhansky and Sturtevant 1938), and these arrangement frequencies were monitored. The different gene arrangements are the result of a phylogeny of mostly overlapping inversions of segments of the third chromosome (Dobzhansky 1944). Because of greatly reduced recombination within the inverted segments in heterokaryotypes, these inversions act to tie together portions of the chromosome into large supergenes. These supergenes (gene arrangements) are inherited and behave in populations as alleles at a single locus. Some natural populations of *D. pseudoobscura* have been sampled repeatedly since the 1930s (Anderson et al. 1975) and provide an excellent historical basis for current research. These continuing geographic surveys over the range of *D. pseudoobscura* have led to the division of the species into five geographic races, each characterized by the gene arrangements present and their frequencies (Dobzhansky and Powell 1975). These races are:

1. Pacific Coast
2. Intermountain Plateau
3. Rocky Mountains and Texas
4. Northern Mexico
5. Southern Mexico and Guatemala

Race 2, the Intermountain Plateau, has been characterized as nearly monomorphic for the Arrowhead (AR) gene arrangement, while the other races are highly polymorphic.

Populations of the Intermountain Plateau were originally sampled and characterized in the early 1940s. Those areas which have been sampled regularly (Bryce Canyon, Utah; Lehman Caves, Nevada; and three localities in Arizona) have remained essentially the same as the original samples (Anderson et al. 1975). During 1976 and 1977 six areas in the northern Intermountain Plateau area were sampled; some of these sites had not been sampled since they were originally characterized in the 1940s and 1950s. This area, which had previously been characterized as nearly monomorphic AR, had undergone great changes both in the particular gene arrangements present and their frequencies (Turner and Jeffery 1980). These populations now have an arrangement array very similar to that found in the Rocky Mountain populations (Race 3) including the endemic Fort Collins arrangement, previously found only in a few areas of the Rocky Mountains. It was hypothesized that these changes came about because of gene flow into these northern Intermountain Plateaus (Race 2) from the Rocky Mountains (Race 3) (Turner and Jeffery 1980).

The release of genes into natural populations has been attempted previously with positive results. Bryant (1976) released *D. pseudoobscura* with a rare esterase allozyme into a small oasis population in Death Valley, California, in an attempt to swamp the population and then determine the amount of immigration in the population. Thirty-eight days after the release, the frequency of the genetic marker had increased from 2% before the release to approximately 80%. Dubinin and Tiniakov (1946) released *D. funebris* with an inversion from another locality into a population where that inversion was rare. The frequency of the released inversion was originally 0.35% and increased to a high of 49.5% approximately one generation after the release. These two results show that it is possible to introduce outside genes or gene arrangements (even those that have been in the laboratory for some time) into a natural population and that they can become integrated into that population at fairly high frequencies.

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This research investigates, through the use of a release experiment, the inversion gene arrangement polymorphism in an Intermountain Plateau population of *Drosophila pseudoobscura*.

MATERIALS AND METHODS

SAMPLING SITES AND METHODS.—Three locations in Bryce Canyon National Park, Utah, were selected as sampling sites. These three sites are separated by distances such that migration by individuals between the sites was thought to be negligible. The southern and northern sampling sites are 14 km apart. The middle site is 5 km from the southern site and 9 km from the northern site. These three areas are quite diverse and probably encompass the entire range of possible *D. pseudoobscura* habitats in Bryce Canyon. The southern sampling site is the least arid and the most similar of the three sites to the northern Intermountain Plateau. Because of this similarity, this site was chosen for the release. During 21–28 June 1978, samples were obtained from each of these three sites. Individual females obtained from nature were used to establish isofemale lines, and F1 larvae were characterized cytologically for the gene arrangement of the third chromosome using standard *Drosophila* salivary techniques.

THE RELEASE.—On the three days immediately following the completion of the initial samples, *D. pseudoobscura* homozygous for Standard (ST), Treeline (TL), or Pikes Peak (PP) gene arrangements were released in the southern sampling area. The flies to be released were grown in large population cages which support approximately 12,000 adult flies. The releases were accomplished by opening these cages and allowing the adults to escape. Thus the released flies were a mixed sample of age and sex, and no attempt was made to release only virgin flies. This was done in five separate release events over the span of three days, one release daily during the evening activity period and on two days releases during the morning activity periods. Approximately equal numbers (approx. 12,000) of each homozygous type were released during each event, and the total number of individuals released was approximately 200,000. No flies were released in the other two sampling sites. All three sites were subsequently sampled and characterized genetically during August 1978 and June, August, and September 1979.

ORIGIN OF RELEASED CHROMOSOMES.—The released PP stock was derived from a collection made in June 1977 at American Fork, Utah. In this collection PP had a frequency of 18.9%. The TL stock came from a collection in Big Cottonwood Canyon, Utah (near Salt Lake City), in June 1977. The frequency of TL in this population was 25.0% (Turner and Jeffery 1980). The ST stocks were from Mather, California, and have been maintained in the laboratory since 1959.

RESULTS AND DISCUSSION

The frequencies of the third chromosome gene arrangements from the initial sample (June 1978) are given in Table 1 along with the totals from previous samples of Bryce Canyon. The June 1978 totals are significantly different from the previous samples total ($X^2 = 13.45$, $p < .01$, 3 df) but not significantly different from the latest (1973) sample of Bryce ($X^2 = 1.51$, $p < .25$, 1 df). The three sample sites have no significant differences in gene arrangement frequencies (Table 1) ($X^2 = 1.4$, $p < .79$, 2 df). The June 1978 samples had two arrangements, Treeline (TL) and Bryce (BR), not previously found in Bryce Canyon samples. The BR arrangement is a new arrangement, an inversion of Arrowhead (AR) with breakpoints 71B and 80C.

The release took place after the June 1978

TABLE 1. Percentage of third chromosome gene arrangements of *D. pseudoobscura* from Bryce Canyon before the release (n = number of chromosomes).

Site	Sampling date	AR	PP	CH	TL	ST	BR	n
Bryce Canyon	1940	96.0	—	2.0	—	2.0	—	100
	1950	92.9	—	2.4	—	4.8	—	84
	1957	93.2	2.6	1.6	—	2.6	—	190
	1965	92.0	1.5	4.0	—	2.5	—	200
	1973	99.3	—	—	—	.7	—	136
	(Anderson et al. 1975)							
Totals		94.6	1.1	2.1	—	2.1	—	710
Bryce Canyon								
Northern site	June 1978	97.8	—	2.2	—	—	—	178
Middle site	June 1978	97.0	—	1.8	0.3	1.0	—	398
Southern site	June 1978	98.4	—	1.0	—	0.3	0.3	304
Totals	June 1978	97.6	—	1.6	0.1	0.6	0.1	880

TABLE 2. Percentage of third chromosome gene arrangements of *D. pseudoobscura* in postrelease samples from Bryce Canyon, Utah (August 1978) (n = number of chromosomes).

Locality	Days since release	AR	CH	ST	PP	TL	SC	n
Northern	day 42 & 43	96.8	2.4	0.8	—	—	—	126
Middle	day 42 & 43	96.0	2.5	0.5	0.5	0.5	—	202
Southern								
	day 40	97.1	—	1.0	1.0	—	1.0	102
	day 41	96.8	1.1	—	—	2.1	—	94
	day 42	90.5	—	1.2	3.6	4.8	—	84

samples and only in the southern site. The populations were sampled again in August 1978 (Table 2). While the nonrelease sites have not changed significantly, the daily gene frequencies from the southern area show the release to have been successful. On days 40 and 41 (since the release), the frequencies (Table 2) are similar to the prerelease samples, but on day 42 the frequency of AR decreased from over 96% the previous day to 90.5%. This decrease in frequency is due to the increased frequencies of the released TL and PP gene arrangements. Again, this decreased AR is not seen in either of the two nonrelease sites even though they were sampled past day 41. These frequency increases are the result of the emergence of the F1 from the released individuals. These data show the released chromosomes (ST, TL, and PP) to have increased from 0.33% in the initial samples to almost 10% 42 days after the release. This appearance 42 days after the release indicates at Bryce Canyon the generation time of 42 days. At this length, these populations could have only three or four generations a year.

From September until April or May temperatures at Bryce Canyon are too cold to support an active *D. pseudoobscura* population. Thus, the next samples following the release were during the summer 1979. Three collections were made, and the gene arrangement frequencies are presented in Table 3. There are no statistically significant differences between samples or sampling sites ($X^2 = .74$, $p < 0.6$, 2 df). Pikes Peak (PP) was the only gene arrangement not seen in the prerelease samples but found in the 1979 samples.

Although a very large number of individuals were released, the resulting change in gene frequencies was small. Reduced survival of the released individuals probably was responsible for a portion of the decline. Dobzhansky and Wright (1943) calculated the survival of released 5–7 day-old orange-eyed *D. pseudoobscura*. They estimated that approximately 90% survive per day. That is probably an overestimate for the current release since some of the released flies were older (and younger) than their samples. Also, Bryce Canyon is 3,000 ft higher in altitude than Dobzhansky and Wright's experimental

TABLE 3. Percentage of third chromosome gene arrangements from sites in Bryce Canyon for summer following August 1978 release (n = number of chromosomes).

Date	Site	AR	CH	ST	PP	n
June 1979	Northern	94.1	—	4.4	1.5	68
	Middle	98.3	0.9	0.9	—	116
	Southern	98.0	1.5	0.5	—	204
	Total	97.4	1.0	1.3	0.3	388
Aug. 1979	Northern	97.2	1.7	1.2	—	176
	Middle	100.0	—	—	—	50
	Southern	97.9	2.1	—	—	144
	Total	97.8	1.6	0.5	—	370
Sept. 1979	Northern	96.2	2.8	—	0.9	106
	Middle	100.0	—	—	—	40
	Southern	93.9	3.8	1.5	0.8	130
	Total	95.7	2.9	0.7	0.7	276
1979	Total	97.1	1.7	0.9	0.3	1034

location. In fact, in their study, when the weather was particularly arid, their recapture rates declined significantly. The increased altitude of Bryce Canyon, with reduced humidity and greater temperature extremes, probably contributes to a survival rate lower than their 90% per day estimate. But, more importantly, in the current release the concern is not on the survival of an individual but the genetic contribution to the next generation. A released female may survive, but unless she can find a suitable oviposition site and sufficient food, she will not contribute genetically to the next generation and the genes she carried will be lost. Laboratory experiments with *D. pseudoobscura* females show over 90% reduction in productivity (number of offspring) under nutritional stress (Turner and Anderson 1983). For these reasons the contributions of released females were probably small in magnitude. In all cases the released chromosomes in the second sample were found as heterozygotes. The contribution of already-mated released females would have been F1 homozygotes. Since virgin females were not released and no homozygotes were found, probably most of the released chromosomes that became integrated into the gene pool were the result of released males mating with wild (AR/AR) females. In retrospect, for a population like Bryce Canyon (one very close to the ecological bounds of the species) a release of males only may be the best strategy.

In the prerelease samples, none of the three sampling sites shows significant differentiation. This lack of spatial differentiation between sites is surprising considering the ecological difference between sites. For instance, only ponderosa pine (*Pinus ponderosa*) is found in all three sampling sites, and it is rare in the southern site. There is also a drop in altitude from the southern site (8,300 ft) to the northern site (7,200 ft). These results may indicate that the Arrowhead arrangement (AR) is responding to some general component of the environment such as temperature. If it were responding to something specific in the environment, different sites with different habitats would be expected to show different frequencies. The homogeneity between sample sites is consistent with the observation that much of the Great Basin *D. pseudoobscura* populations are characterized by a high frequency of the AR arrangement (Anderson et al. 1975, Dobzhansky and Powell 1975).

One other interesting aspect of these samples (August 1978, Table 2) is the appearance of the Santa Cruz (SC) gene arrangement at Bryce Canyon. This arrangement was not in the release, and its appearance at this time is only coincidental. This arrangement is usually found along the Pacific Coast of California and in southern Mexico. In previous samples of almost 1,600 chromosomes (Table 1) SC had never been identified at Bryce. In samples from related areas (Nevada, Arizona, and Utah) (Anderson et al. 1975, Turner and Jeffery 1980), nearly 5,000 chromosomes have been characterized and SC has never been identified in this region. Whether SC has always been at Bryce but in extremely low frequency or whether this SC came with an individual immigrant (active or passive) fly from a population where the SC arrangement is found cannot be determined at this time, although the latter seems the more probable alternative.

TL, which had reached levels close to 5% in the southern sampling area 42 days following the release (Table 2), was not observed in over 1,000 chromosomes examined in 1979, of which almost 500 came from the southern (release) area (Table 3). A second gene arrangement in the release, Standard (ST), did not show a significant increase in postrelease samples (Table 2) and had approximately the same frequency in 1979 (Table 3) as that seen in the 1978 prerelease samples (Table 1). In the June 1979 sample from the northern site, Standard has a frequency of 4.4% (Table 3), but it decreased and was not found in the August 1979 sample from this site. Standard did not show a frequency increase in the release area (Tables 1, 2). The observation from the northern site could be the result of migration of the released flies (or their offspring) to the northern site or the result of sampling error due to small sample sizes. The results of these two arrangements (TL and ST) are similar and consistent with no long-term effect of the release.

The PP gene arrangement had not been found in Bryce since 1964, but it did reach a level of 3.6% following the release (Table 2) and was found in low frequency (0.3%) in 1979. During the 1979 samples PP was found in all three sample sites and is most probably a low-level retention following the incorporation of the released PP arrangement into the Bryce Canyon gene pool. This result would indicate that the earlier assumption that the sites were far enough apart to ignore migration was incorrect. In the two to three generations since the release all three sites have two (PP and ST) of the three released arrangements, a linear distance of 14 km. With this level of migration we can consider this area as supporting one large breeding population. In this large population an introduced gene (released or migrant) may be swamped by the local (AR) gene pool, without being able to enter a small isolate and increase in frequency (as the result of either stochastic or selective mechanisms). This type of population structure would minimize the effects of migration in changing gene frequencies.

Additionally, to persist in this population, an arrangement (or gene) must survive the winter. When high-elevation populations overwinter, they undergo a severe bottleneck in population size because of the low temperatures. How *D. pseudoobscura* overwinter is not known, but overwintering is unquestionably a severe process. In laboratory experiments on overwintering ability only a small frequency of the flies survive cold shocks of just a few days (Jefferson et al. 1974), and over a winter of six to eight months only a very small number of individuals may survive. In this way, the released arrangements may not survive the winter and the sampling effect of the resultant population bottleneck. This bottleneck would eventually cause the population to lose variability through genetic drift. These results also bear on the question of overwintering; that is, whether these higher-altitude populations overwinter in place (at altitude) rather than be repopulated each spring from lower-altitude overwintering refugia. The latter hypothesis is similar to that observed in the desert populations of *D. pseudoobscura* where populations are refounded each year from neighboring mountains after the hot summers have eliminated the populations (Jones et al. 1981). The persistence of the Pikes Peak (PP) arrangement would be consistent with an overwintering-in-place hypothesis and not a repopulation each spring from lower-altitude populations.

A decrease in frequency due to small fitness differences would take many generations. The PP and TL arrangements were isolated from areas with an environment and elevation roughly similar to Bryce Canyon. Both arrangements were in relatively high frequency where found originally, PP being almost 20% and TL 25%. Thus, if fitness differences do exist between the released chromosomes and the native AR, they most likely would be small. Since *D. pseudoobscura* do not reproduce during the winter, from August 1978 until June 1979 there is only one generation and at most two. The rapidity of the decrease would suggest that if the decrease were due to an inherent selective disadvantage, this fitness difference must be extremely large. The rapid decrease would seem more consistent with the swamping effect of a large population size and random drift in overwintering populations.

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ROBBER FLIES OF UTAH (DIPTERA: ASILIDAE)

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ABSTRACT.—Reported are 158 species of Asilidae (Diptera) in 50 genera from Utah. Keys to subfamilies, genera, and species are given, along with information on seasonal and distributional occurrence in Utah. Seventy-six maps and 56 line drawings show the Utah distribution of each species and illustrate important characters used in the keys. A table summarizes the current status of names used in earlier state lists.

The Asilidae (Diptera) have long attracted the attention of collectors. As a result, numerous specimens have been deposited in collections in the state of Utah. The systematics of the family have been studied rather intensively so that the taxonomic status of most groups is known. The purpose of this study is to assemble the numerous records and to identify the species of asilids caught in Utah.

The catalog of Diptera (Stone et al. 1965) shows that about 50 species of asilids are either listed as occurring in Utah or are included in the broad geographical ranges delineated under a given species. A preliminary examination of the specimens from the Utah State University Entomological Museum revealed that identifications made by prominent workers of the family existed for over 150 different species. A careful examination of collections of asilids from the state revealed 158 species in 50 genera.

REVIEW OF LITERATURE

Brown (1929) published the first paper dealing with Asilidae of Utah. He listed 22 species of robber flies as occurring in Utah, one of which was not determined to species. He included drawings of the genitalia of most of these species. Table 1 summarizes the current status of the species listed by Brown (1929).

Knowlton and Harmston (1938) published a list of Asilidae found in Utah. A summary of the current status of these species is given in Table 2.

A further list of asilids captured in Utah was given by Knowlton, Harmston, and Stains

TABLE 1. Current status of species listed in Brown (1929).

1.	*Ospriocerus abdominalia* (Say)	= *O. abdominalis*
2.	*Stenopogon modestus* Loew	= *S. inquinatus*
3.	*Stenopogon consanguineus* Loew	Specimens are *Scleropogon neglectus*
4.	*Stenopogon californiae* (Walker)	Specimens are *S. rufibarbis*
5.	*Stenopogon* sp. female	Not enough information
6.	*Heteropogon ludius* (Coquillett)	Wilcox lists as *H. senilis*
7.	*Dasyllis fernaldi* Back	= *Laphria fernaldi*
8.	*Deromyia bigoti* (Bellardi)	= *Diogmites grossus*
9.	*Proctacanthus arno* Townsend	= *P. nearno*
10.	*Erax barbatus* (Fabricius)	= *Efferia albibarbis*
11.	*Erax interruptus* (Macquart)	= *Triorla interrupta*
12.	*Erax stamineus* Williston	= *Efferia staminea*
13.	*Erax subpilosus* Schaeffer	Neither Wilcox (1966) nor I saw specimens of this species.
14.	*Mallophora fulviventris* Macquart	Unrecognizable to Cole and Pritchard (1964).
15.	*Mallophora guildiana* Williston	= *Megaphorus guildiana*
16.	*Promachus bastardii* (Macquart)	= *P. dimidiatus*
17.	*Promachus nigripes* Hine	Specimens are *P. aldrichii*.
18.	*Asilus lecythus* Walker	Utah specimens are *Machimus occidentalis*.
19.	*Asilus tenebrosus* Williston	= *Machimus griseus*

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TABLE 2. Changes in status of species listed in Knowlton and Harmston (1938).

1. *Ablautus trifarius* Loew	Utah specimen is *Omninablautus nigronotum*
2. *Andrenosoma abdominalis* (Brown)	= *Cerotainiops abdominalis*
3. *Asilus callidus*	= *Machimus callidus*
4. *A. compositus* Hine	= *Polacantha composita*
5. *A. erythrocnemius* Hine	Specimens are *Machimus paropus*
6. *A. gracilus* Weidemann	Specimens are *Polacantha composita*
7. *A. mesae* Tucker	= *Negasilus mesae*
8. *A. occidentalis* Hine	= *Machimus occidentalis*
9. *A. tenebrosus* Williston	= *Machimus griseus*
10. *Bombomima fernaldi* (Back)	= *Laphria fernaldi*
11. *Cyrtopogon callipedilus* Loew	No specimens seen; this is a California species; Utah specimens were probably *C. montanus*
12. *Deromyia bigoti* Bellardi	*Diogmites grossus*
13. *Dioctria parvula* Coquillett	Probably *D. henshawi*
14. *Efferia candida* Coquillett	Specimen is *E. benedicti*
15. *Erax* spp.	*Efferia* spp.
16. *Erax argyrosoma* Hine	Utah specimens are *Efferia benedicti*
17. *Erax barbatus* Fabricius	= *Efferia albibarbis*
18. *E. californicus*	No specimen seen, specimen was probably *Efferia benedicti*
19. *E. dubius* Williston	Nomen nudum
20. *E. interruptus*	= *Triorla interrupta*
21. *E. knowltoni* Bromley	= *Efferia benedicti*
22. *E. pallidulus* Hine	Not seen in collections
23. *E. texana* Banks	Not seen in collections
24. *Eucyrtopogon maculosus* Coquillett	No specimen seen
25. *Heteropogon lautus* Loew	Utah specimen is *H. maculinervis*
26. *Mallophora guildiana* Williston	= *Megaphorus guildiana*
27. *Mallophora fautricoides* Curran	= *Mallophora fautrix*
28. *Neoitamus hardyi* Bromley	= *Asilus auriannulatus*
29. *Nicocles punctipennis* Melander	= *N. utahensis*
30. *Ospriocerus ventralis* (Say)	= *O. abdominalis*
31. *Proctacanthus arno* Townsend	= *P. nearno*
32. *P. cacopiloga* Hine	= *Proctacanthella cacopiloga*
33. *Promachus nigripes* Hine	Utah specimens are *P. aldrichii*
34. *P. quadratus* Weidemann	Eastern species; Utah specimen is *P. dimidiatus*
35. *Scleropogon longulus* Loew	= *Ospriocerus longulus*
36. *Stenopogon helvolus* Loew	Specimen is *Scleropogon indistinctus*
37. *Stenopogon neglectus* Bromley	= *Scleropogon neglectus*
38. *Stenopogon obscuriventris* Loew	Utah specimens are *S. martini*
39. *S. picticornis* Loew	= *Scleropogon picticornis*

(1939). A review of the species from that publication and their current status is given in Table 3.

Johnson's (1936) unpublished master's thesis is an important contribution to the study of the fauna of the state. He listed 73 species as occurring in Utah. Table 4 summarizes the changes in the status of the species listed in Johnson (1936). Johnson's specimens are in the Brigham Young University collection and were examined during this study.

Numerous other records of asilids caught in Utah are scattered throughout the literature. These are listed unmarked under the discussions of individual species.

METHODS

Utah collections of Asilidae were examined at Utah State University, Brigham Young University, the University of Utah, Southern Utah State College, Dixie College, and the College of Eastern Utah. Additionally, a search through literature dealing with Asilidae was made, and records of specimens collected in Utah were included in the synopsis of each species.

Numerous areas throughout the state were visited, and extensive collections of Asilidae were made during this study. Areas which received particular attention were: Washing-

TABLE 3. Changes in status of species listed in Knowlton, Harmston, and Stains (1939).

1. *Anisopogon lautus* Loew	Probably *Heteropogon senilis*
2. *Asilus avidus* Van der Wulp	Specimens are *Machimus adustus*
3. *A. belli* Curran	= *Negasilus belli*
4. *A. delicatulus* Hine	Specimen unidentifiable
5. *A. erythrocnemius* Hine	Specimens are *Machimus paropus*
6. *A. occidentalis* Hine	= *Machimus occidentalis*
7. *A. paropus* Walker	= *Machimus paropus*
8. *Bombomima fernaldi* Back	= *Laphria fernaldi*
9. *Dioctria pleuralis* Banks	Specimens are *Dioctria vera*
10. *Efferia candida* Coquillett	Specimens are *E. davisi*
11. *Erax barbatus* Fabricius	= *Efferia albibarbis*
12. *E. bicaudatus*	Specimens are *Efferia frewingi*
13. *E. dubius* Williston	Nomen nudum
14. *E. zonatus* Hine	= *Efferia zonata*
15. *Holopogon phaeonotus* Loew	Specimens are *H. albipilosus*
16. *H. seniculus* Loew	Specimens are *H. albipilosus*
17. *Laphystia sexfasciatus* Say	Specimen is *L. tolandi*
18. *Mallophora bromleyi* Curran	= *M. fautrix*
19. *M. purdens* Pritchard	= *Megaphorus willistoni*
20. *M. pulchra* Pritchard	= *Megaphorus pulcher*
21. *Neoitamus hardyi* Bromley	= *Asilus auriannulatus*
22. *Nicocles punctipennis* Melander	= *N. utahensis*
23. *Ospriocerus ventralis* Coquillett	= *O. abdominalis* (Say)
24. *Proctacanthus arno* Townsend	= *P. nearno* Martin
25. *Promachus nigripes* Hine	Specimens are *P. aldrichii*
26. *Stenopogon helvolus* Loew	Specimens are *Scleropogon coyote*
27. *Stenopogon neglectus* Bromley	= *Scleropogon neglectus*
28. *Stenopogon obscuriventris* Loew	Specimens are *S. martini*
29. *S. picticornis* Loew	= *S. picticornis*

ton County, the only area of the state where species of Mohave Desert origins could be collected; the Raft River Mountains; Cache County; Box Elder County; Juab County; Emery County; Grand County; and San Juan County.

The taxonomic synopsis presented in this paper consists of information regarding original citation and author, type locality, type repository, all of which were obtained from the literature. The county and seasonal distributions of each species were taken from specimen labels. The seasonal distributional data are expressed as a range of earliest and latest known collection dates for Utah specimens.

Keys to subfamilies, genera, and species were constructed using published information and new insights. A map was produced showing the distribution of each species listed, and 56 figures were drawn using a camera lucida on a Wild M8 stereomicroscope. The figures illustrate important characters used in the keys.

KEYS

Key to the Subfamilies of Utah Asilidae

1. R_{2+3} ending in costa (Figs. 40, 46) 2

— R_{2+3} joining R_1, closing cell r_1 (Fig. 43) 3

2(1). Abdominal segment 2 elongate, five or more times as long as wide; resembling, somewhat, small damselflies .... Leptogastrinae

— Abdominal segment 2 shorter, not more than five times as long as wide; not particularly resembling damselflies .... Dasypogoninae

3(2). Antennae without a terminal style, ending bluntly .... Laphriinae

— Antennae bearing a terminal style .... Asilinae

Key to the Genera of Utah Leptogastrinae and Dasypogoninae

(Modified from Wood 1981)

1. Abdominal segment 2 elongate, five or more times as long as wide; abdomen very thin and elongate .... *Leptogaster* Meigen[2]

— Abdominal segment 2 shorter, not more than five times as long as wide; abdomen generally shorter and stout 2

2(1). Foretibia bearing a terminal, clawlike spur on ventral surface which is thicker and sigmoid (Figs. 54–55) 3

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[2] Much difficulty was met using the key given by Martin (1957). Although several species of *Leptogaster* are present in Utah collections, reliable species determinations were not made. The distribution of this genus in Utah is given in Fig. 100.

TABLE 4. Changes in status of species listed in Johnson (1936).

1. *Ablautus squamipes* Cole	Specimens are *A. mimus*
2. *Andrenosoma similis* (Brown)	= *Cerotainiops abdominalis*
3. *Asilus avidus* Van der Wulp	Specimens are *Machimus adustus*
4. *A. brevicomus* Hine	= *Neoitamus brevicomus*
5. *A. mesae* (Tucker)	= *Negasilus mesae*
6. *A. occidentalis* Hine	= *Machimus occidentalis*
7. *A. paropus* Walker	= *Machimus paropus*
8. *A. tenebrosus* Williston	Specimens are *Machimus griseus*
9. *Bombomima fernaldi* (Back)	= *Laphria fernaldi*
10. *Chrysoceria pictitarsis* (Bigot)	= *Callinicus pictitarsis*
11. *Cophura texana* Bromley	No specimens seen
12. *Cyrtopogon dasyllis* Williston	Specimens are *C. dasylloides*
13. *C. leucozona* Loew	= *C. montanus*
14. *C. nugator* Osten Sacken	Specimens are *C. banksi*
15. *Diogmites pulchra* (Back)	Specimens are *Diogmites grossus*
16. *Ecthopoda* sp.	No label; spelling *Ecthodopa*
17. *Erax argyrosoma* (Hine)	Specimens are *Efferia benedicti*
18. *Erax barbatus* Fabricius	= *Efferia albibarbis* (Macquart)
19. *Erax bicaudatus* Hine	Probably *Efferia frewingi*
20. *Erax candidus* (Coquillett)	Specimens are *Efferia davisi*
21. *Erax canellus* Bromley	Specimens are *Efferia benedicti*
22. *Erax cingulatus* Bellardi	No specimens seen; not Nearctic
23. *Erax dubius* (Williston)	Nomen nudum
24. *Erax interruptus* (Macquart)	= *Triorla interrupta*
25. *Erax pilosus* Hine	No specimens seen
26. *Erax stramineus* Williston	Specimens are *Efferia benedicti*
27. *Holopogon seniculus* Loew	Specimens are *Holopogon albipilosus*
28. *Laphystia limatulus* Coquillett	Specimen is *Laphystia rubra*
29. *L. rufiventris* Curran	Specimens are *Laphystia tolandi*
30. *Lestomyia fraudigera* Williston	Specimen is *Lestomyia sabulona*
31. *Mallophora bromleyi* Curran	= *Mallophora fautrix*
32. *Proctacanthella leucopogon* (Will.)	No specimens seen
33. *Proctacanthus arno* Townsend	= *Proctacanthus nearno*
34. *Promachus bastardii* (Macquart)	Damaged; probably *P. dimidiatus*
35. *P. nigripes* Hine	Specimens are *P. aldrichii*
36. *Stenopogon californiae* (Walker)	Specimens are *S. rufibarbis*
37. *S. helvolus* (Loew)	Probably *Scleropogon neglectus*
38. *S. obscuriventris* Loew	Specimens are *S. rufibarbis*

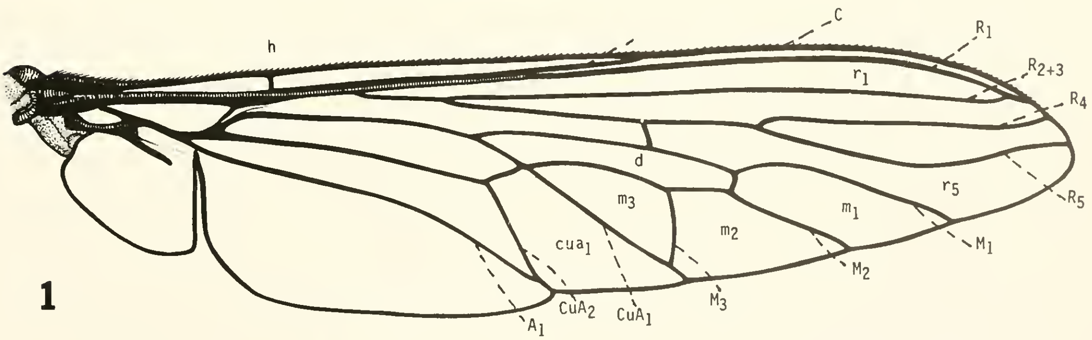

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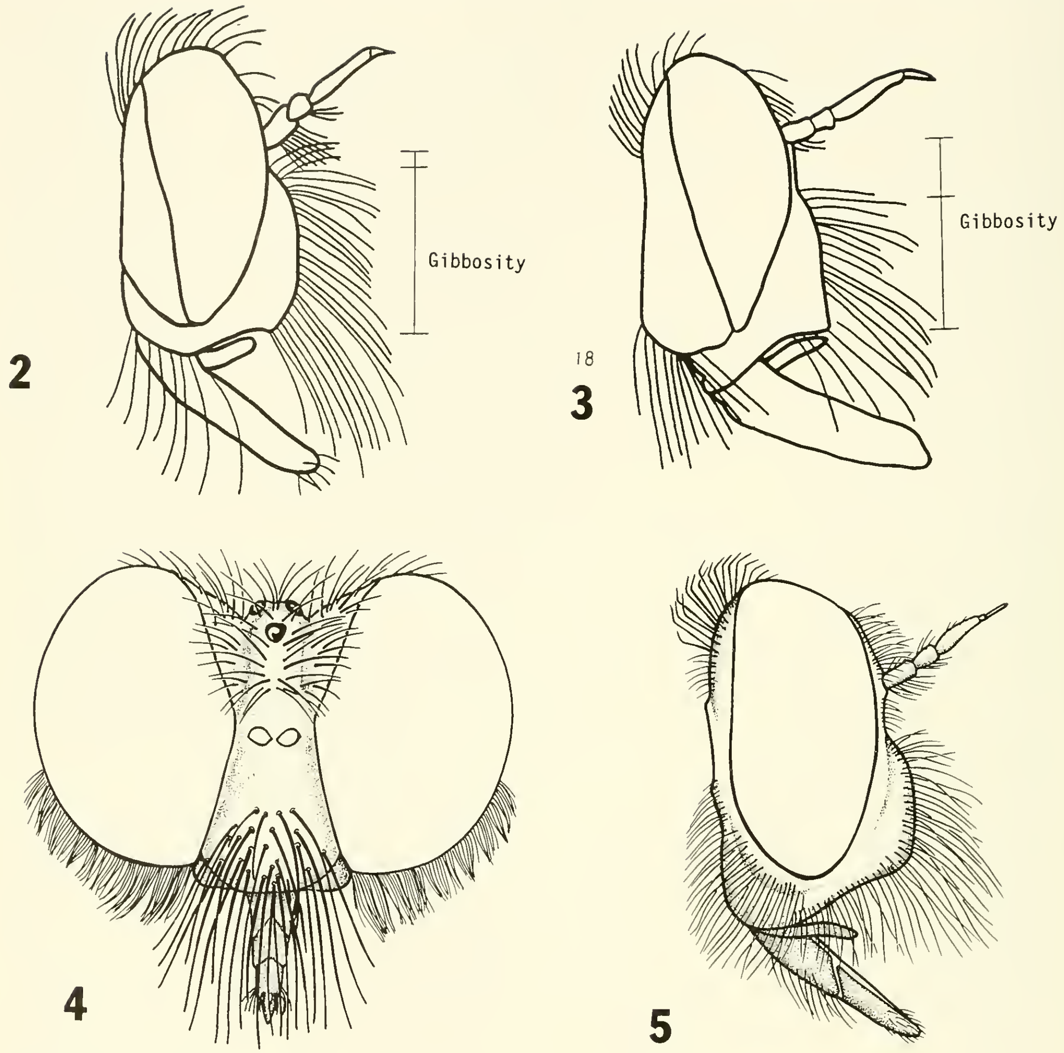
Fig. 1. *Proctacanthus nearno* Martin, right wing: A_1, first anal vein; C, costa; CuA_1, first anterior branch of cubitus; cua_1, anterior cubital cell; CuA_2, second anterior branch of cubitus; d, discal cell; h, humeral crossvein; M_1, first branch of media; m_1, first medial cell; M_2, second branch of media; m_2, second medial cell; M_3, third branch of media; m_3, third medial cell; R_1, first branch of radius; r_1, first radial cell; R_{2+3}, fusion of second and third branches of radius; r_3, third radial cell; R_4, fourth branch of radius; r_4, fourth radial cell; R_5, fifth branch of radius; r_5, fifth radial cell; Sc, subcosta.



Figs. 2–5. Heads of Utah Asilidae: 2, *Stenopogon rufibarbis* Bromley, lateral aspect; 3, *Stenopogon inquinatus* Loew, lateral aspect; 4, *Lasiopogon monticola* Melander, cephalic aspect; 5, *Neoitamus brevicomus* (Hine), lateral aspect.

— Foretibia without a terminal differentiated spur on ventral surface 12

3(2). Differentiated spur of foretibia meeting a raised denticulate area on basitarsus (Fig. 54) 4

— Differentiated spur of foretibia not meeting a differentiated denticulate area on basitarsus (Fig. 55) 7

4(3). Face inflated and haired on lower two-thirds . . . . . . *Lestomyia sabulona* Osten Sacken

— Face flat, hair confined to lower one-third . . . 5

5(4). Cell m_3 open; two flagellomeres present, the second being small, bearing a pit with apical bristle . . . . *Saropogon mohawki* Wilcox

— Cell m_3 closed; one flagellomere 6

6(5). Scutellar bristles present . . . . . *Diogmites* Loew

— Scutellar bristles absent . . . . *Blepharepium sonorensis* Papavero & Bernardi

7(3). Pulvilli present 8

— Pulvilli absent 11

8(7). Face inflated on lower two-thirds or more; anterior mesonotum bearing a manelike crest of hairs on midline . . . . *Comantella* Curran

— Face flat or slightly rounded; mesonotal crest absent 9

9(8). Style of antenna anteapical, in a notch at about midlength of dorsal surface of flagellomere 1; abdomen pitted . . . *Taracticus ruficaudus* Curran

— Style apical; abdomen not pitted 10

10(9). Wings with distinct spots on most crossveins and furcations, otherwise hyaline; male with only six visible tergites, last two visible tergites widened and covered with dense silvery pollen .... *Nicocles* Jaennicke

— Wings hyaline more washed with brown, spots, if present, indistinct .... *Cophura* Osten Sacken

11(7). Presutural dorsocentral bristles present; length less than 5 mm .... *Omninablautus nigronotum* Wilcox

— Presutural dorsocentral bristles absent; length greater than 7 mm .... *Hodophylax basingeri* Pritchard

12(2). Sides of frons greatly divergent toward vertex (Fig. 4) 13

— Sides of frons subparallel or converging toward vertex 14

13(12). Face strongly inflated and haired on lower three-fourths .... *Lasiopogon* Loew

— Face but slightly convex; mystax confined to lower margin .... *Stichopogon* Loew

14(12). Face and frons narrow; head about as wide as high and appearing small in proportion to thorax 15

— Face and frons wider; head wider than high . 17

15(14). Hypopleuron (katatergite) lacking bristles or hairs (Fig. 31) .... *Stenopogon* Loew

— Hypopleuron bearing bristles or hairs (Fig. 30) 16

16(15). Flagellomere 1 at most one and three-fourths length of antennal segments 1 and 2 combined; long, slender terminal style present . ... *Scleropogon* Loew

— Flagellomere 1 at least two times length of antennal segments 1 and 2 combined; terminal style, if present, short ... *Ospriocerus* Loew

17(14). R_{2+3} bent sharply forward near apex, making nearly a 90 degree angle with wing margin (Fig. 45) .... *Laphystia* Loew

— R_{2+3} not bent sharply forward to make such an angle with wing margin (Fig. 40) 18

18(17). Basal half of wing darkened; eyes set off from face along lower margin by grooves running along vertical margin of eyes; CuA_2 and A_1 fused before wing margin .... *Haplopogon utahensis* Wilcox

— Basal half of wing not darkened, although may be spotted; eyes not set off by vertical grooves; CuA_2 and A_1 not joining before wing margin (except in *Myelaphus*) 19

19(18). Mystax limited to lower one-third of face or with only a few hairs near antennae in addition to lower mystax 20

— Mystax extending more than halfway up face 22

20(19). Hind femur and tibia club-shaped; R_4 reaching wing margin anterior to wing tip .... *Dioctria* Meigen

— Hind femur and tibia not club-shaped, at most slightly expanded near apex 21

21(20). Flagellomeres 1 and 2 lobed at apex .... *Myelaphus lobicornis* Osten Sacken

— All flagellomeres simple, not lobed .... *Dicolonus sparsipilosum* Back

22(19). Pulvilli absent; flattened, scalelike hairs present on thorax, legs, and wing base .... *Ablautus* Loew

— Pulvilli present; scalelike hairs absent 23

23(22). Midtibia bearing a pair of stout spines at apex which are directed outward at an angle near 90 degrees .... *Callinicus* Loew

— Midtibia with all apical spines directed distally 24

24(23). Wing with dark spot on r-m, furcation of R_4 and R_5 and at apex of cell d, other spots may also be present 25

— Wings hyaline or darkened; spot pattern not as above 26

25(24). Presutural dorsocentral bristles stout; mesonotum strongly arched .... *Metapogon carinatus* Wilcox

— Presutural dorsocentral bristles absent; mesonotum not strongly arched .... *Eucyrtopogon* Curran

26(24). Face strongly inflated, extending greater than length of scape past eye margin when viewed from the side 27

— Face flat or but slightly convex 29

27(26). Dorsocentrals weak, hairlike .... *Cyrtopogon* Loew

— Dorsocentrals bristlelike, prominent 28

28(27). Mystax composed of bristles; male with wing tip darkened and basal half of wing covered with white bloom ... *Coleomyia alticola* James

— Mystax composed of weak hairs; wings of both sexes hyaline .... *Nannocyrtopogon aristatus* James

29(26). Hind tibia club-shaped, broadest near apex, as thick as or thicker than hind femur .... *Holopogon* Loew

— Hind tibia not club-shaped but spindle-shaped or straight, broadest near middle, thinner than hind femur 30

30(29). Hairs of thorax branched .. *Heteropogon* Loew

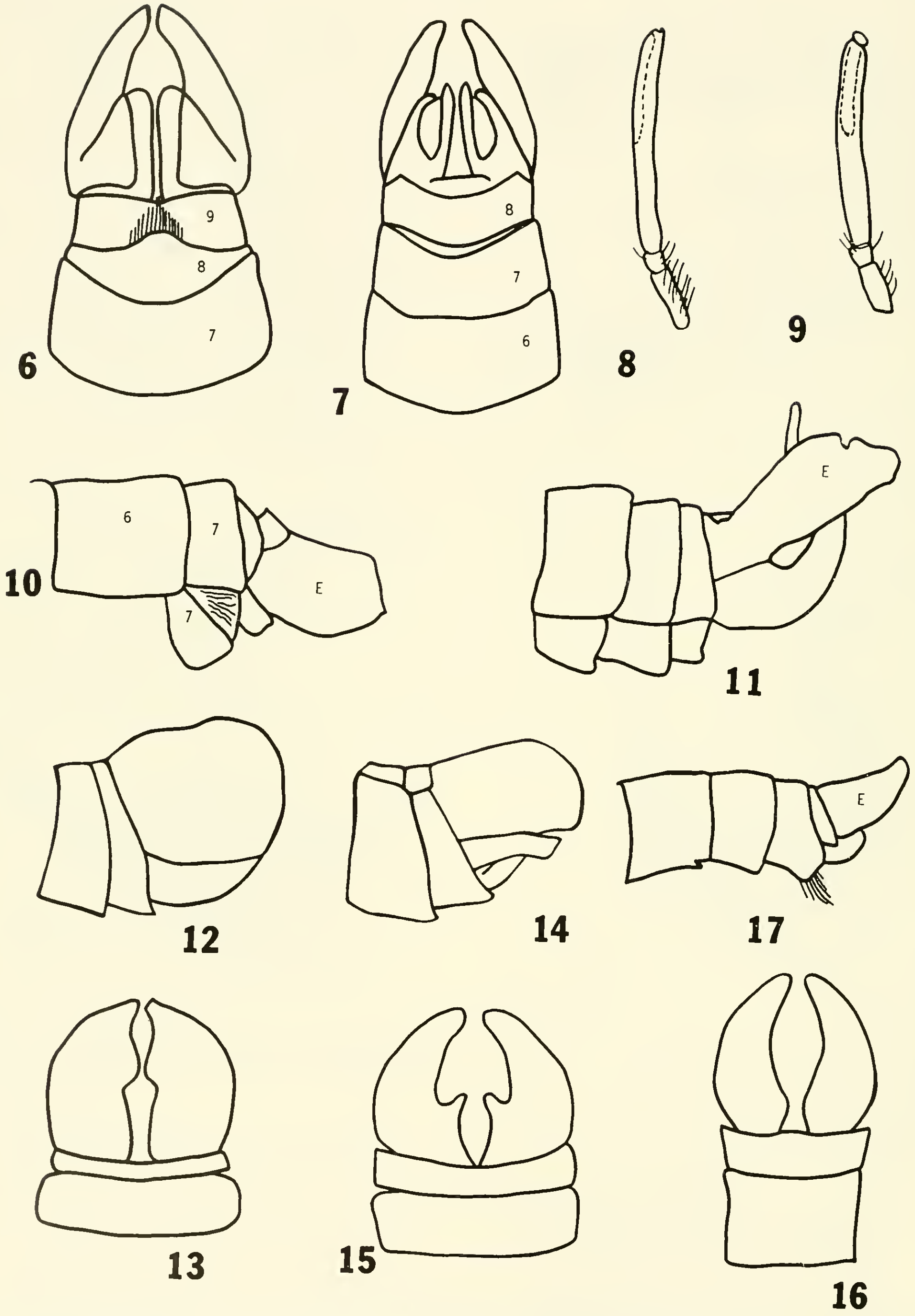
— Hairs of thorax straight or crinkled, not branched 31

31(30). Legs and tergites with greenish metallic reflections .... *Sintoria cazieri* Wilcox

— Legs and tergites without metallic reflections .... *Wilcoxia painteri* Wilcox

Key to the Species of Utah *Ablautus* Loew Including *Omninablautus* Pritchard

(Modified from Wilcox 1966c)



Figs. 6–17. Utah Asilidae: 6, male genitalia of *Machimus occidentalis* (Hine), ventral aspect; 7, male genitalia of *Machimus callidus* (Williston), ventral aspect; 8, antenna of *Ospriocerus abdominalis* (Say); 9, antenna of *Ospriocerus vallensis* Martin; 10, male genitalia of *Regasilus blantoni* Bromley, lateral aspect, E = epandrium; 11, male genitalia of *Neomochtherus lepidus* (Hine), lateral aspect, E = notched epandrium; 12, male genitalia of *Lasiopogon aldrichii* Melander, lateral aspect; 13, surstyli of *Lasiopogon aldrichii* Melander from below; 14, male genitalia of *Lasiopogon monticola* Melander, lateral aspect; 15, surstyli of *Lasiopogon monticola* Melander from below; 16, surstyli of *Lasiopogon cinereus* Cole from below; 17, male genitalia of *Asilus auriannulatus* (Hine), lateral aspect, E = epandrium.

1. Mesonotum with black, shining spots on sides . . . . *Omninablautus nigronotum* Wilcox

— Mesonotum entirely pollinose 2

2(1). Face, frons, thorax, and legs without scalelike hairs 3

— Face, frons, thorax, and legs with scalelike hairs 4

3(2). Frons golden brown pollinose, male with scalelike hairs of foretarsi black laterally and pale brown medially, hind tibia and femur black . . . . *mimus* Osten Sacken

— Frons white pollinose, male with scalelike hairs of foretarsi all brown, apex of hind femur and middle of hind tibia reddish . . . . *rufotibialis* Back

4(2). Frons white or slightly yellowish pollinose, scalelike hairs above antennae on frons not limited to margins of eyes . . . . *flavipes* Coquillett

— Frons golden brown pollinose; scale hairs of frons limited to margins of eyes . *coquilletti* Wilcox

Key to the Species of Utah *Callinicus* Loew

(Modified from Wilcox 1936a)

1. Femora black, central stripe of mesonotum reaching scutellum, presutural black spots extending to the lateral margins . . . . *pollenius* Cole

— Femora yellow, central stripe of mesonotum reaching scutellum, presutural black spots small and isolated from lateral margin by golden pollen . . . . *pictitarsis* Bigot

Key to the Species of Utah *Comantella* Curran

(Modified from James 1937b)

1. Style one-third as long as antennal segment 3; venter black-haired, at least on anterior segments 2

— Style one-half as long as antennal segment 3; venter with all hairs white . . . . . . *pacifica* Curran

2(1). Thoracic mane set on a well-defined black vitta; hairs of mystax black on entire length . . . . *rotgeri* James

— Thoracic mane set on poorly defined black vitta; hairs of mystax with tips white . . . . *fallei* (Back)

Key to the Species of Utah *Cophura* Osten Sacken

(Modified from Pritchard 1943)

1. Scutellum entirely pollinose, base of tibia with dark yellow band . . . . *pollinosa* Curran

— Scutellum shining black, base of tibia without dark yellow band 2

2(1). Wings hyaline . . . . *albosetosa* Hine

— Wings brownish 3

3(2). Scutellum clothed with short, stout, dark bristles . . . . *brevicornis* (Williston)

— Scutellum clothed with long, thin, light hairs . . . . *scitula* (Williston)

Key to the Species of Utah *Cyrtopogon* Loew

(Modified from Wilcox and Martin 1936)

1. Last segment of male foretarsus extremely flattened . . . . *albifacies* Johnson

— Last segment of male foretarsus not flattened 2

2(1). Scutellum convex, mostly shining; face usually strongly gibbous; antennae situated at about three-fourths height of head; more densely pilose and less pollinose species 3

— Scutellum flattened, largely or entirely pollinose; face not usually strongly gibbose; antennae situated at about one-half height of head; less pilose and more pollinose species 13

3(2). Antennal segment 3 yellowish red 4

— Antennal segment 3 black or dark brown 5

4(3). Abdomen with yellowish orange hairs, denser in male; pollinose fasciae of abdomen yellowish; mystax mostly golden; length 9–12 mm . . . . *auratus* Cole

— Abdomen with hairs light yellowish silver; pollinose fasciae of abdomen silver; mystax whitish yellow with much black; length 10–15 mm . . . . *pulcher* Back

5(3). Abdomen with dense orange-yellow hairs on dorsum 6

— Abdomen with dense hairs (may be somewhat yellowish or black) limited to the lateral margins 7

6(5). Orange hairs of abdomen limited to segments 1–4 . . . . *curtistylus* Curran

— Orange hairs of abdomen on at least segments 1–5 . . . . *dasylloides* Williston

7(5). Male with disc of broad black hairs on at least apical two segments of midtarsus; foretarsal segments 2–5 of male with a differentiated, dense, narrow fringe of silvery hairs 8

— Male without disc of black hairs on apical two segments of midtarsus; foretarsus of male without a differentiated fringe of silvery hairs 9

8(7). Long hairs of lateral margins of abdomen entirely yellowish white . . . *plausor* Osten Sacken

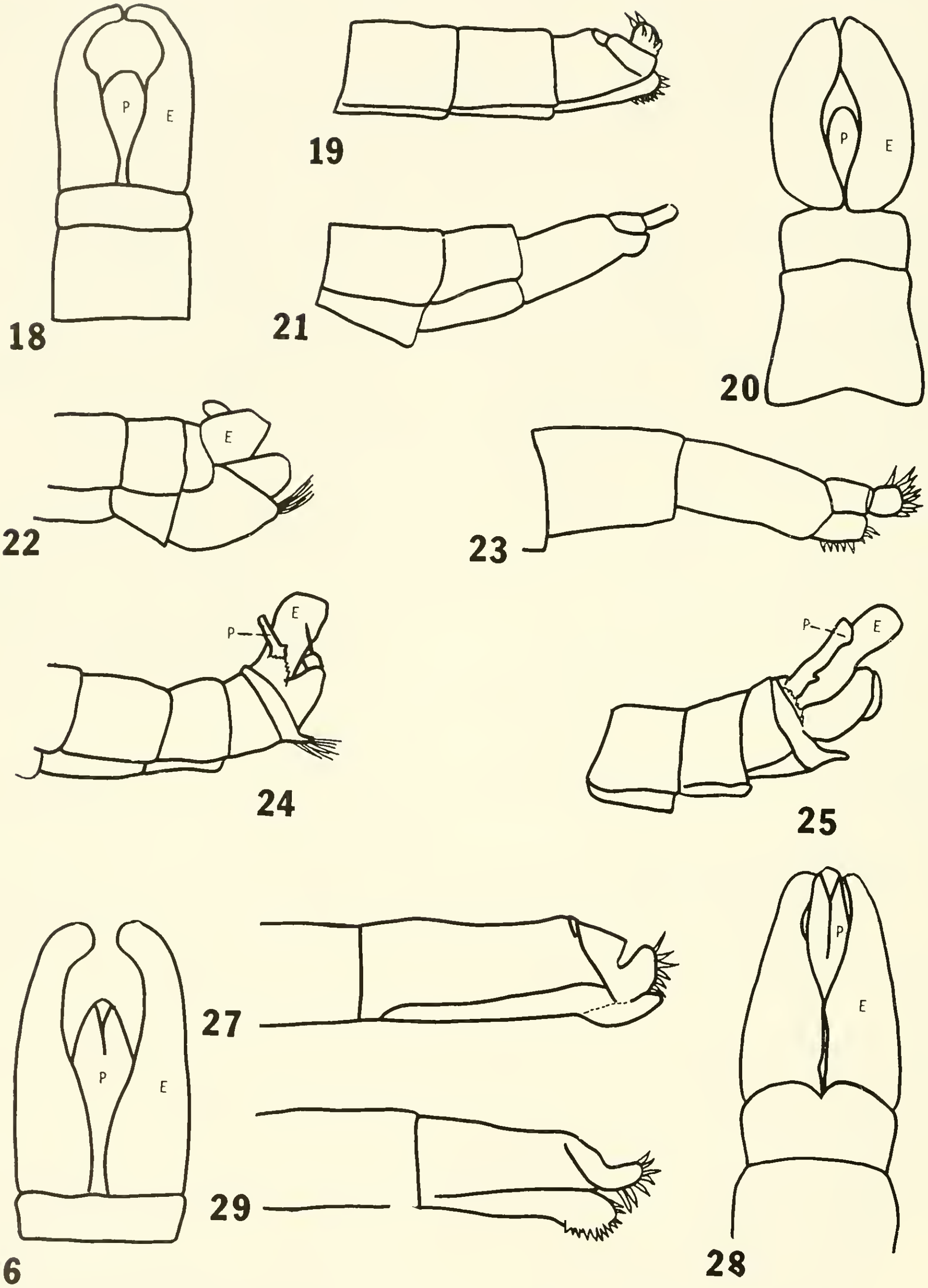
— Long hairs of lateral margins of abdomen in part black . . . . *willistoni* Curran

9(7). Wing of male with apex black, apex of anal cell also black; wing of female darkened somewhat in same areas; pleura largely shining . . . . *bimacula* Walker

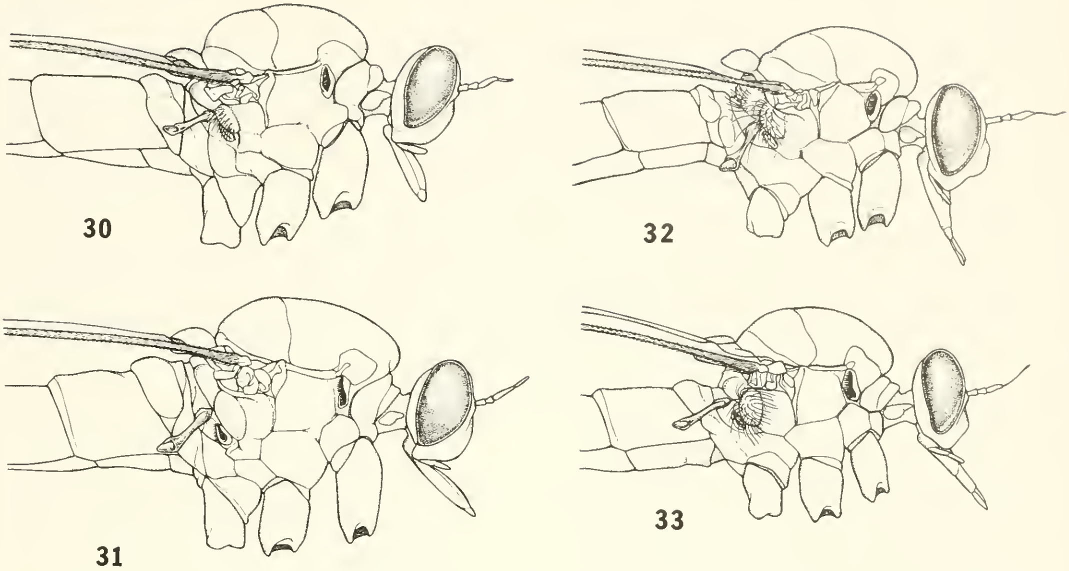
— Wing without black spots; pleura extensively pollinose 10

10(9). Tibiae and tarsi more or less reddish, at least below, rarely male with only underside of tarsi reddish 11

— Tibiae and tarsi either both black or with tibiae all black and foretarsi yellow with white hairs 12



Figs. 18–29. Utah Asilidae, terminalia: 18, male genitalia of *Philonicus arizonensis* (Williston), dorsal aspect, E = epandrium, P = proctiger; 19, female genitalia of *Philonicus arizonensis* (Williston), lateral aspect; 20, male genitalia of *Polacantha composita* (Hine), dorsal aspect, E = epandrium, P = proctiger; 21, female genitalia of *Polacantha composita* (Hine), lateral aspect; 22, male genitalia of *Proctacanthella cacopiloga* (Hine), lateral aspect, E = epandrium; 23, female genitalia of *Proctacanthella cacopiloga* (Hine), lateral aspect; 24, male genitalia of *Machimus griseus* Hine, lateral aspect, with left epandrium removed, E = epandrium unnotched, P = proctiger without ventral process; 25, male genitalia of *Machimus adustus* Martin, lateral aspect, with left epandrium removed, E = epandrium, P = proctiger with ventral process; 26, male genitalia of *Proctacanthus nearno* Martin, dorsal aspect, E = epandrium, P = proctiger; 27, female terminalia of *Proctacanthus nearno* Martin, lateral aspect; 28, male genitalia of *Proctacanthus micans* Schiner, dorsal aspect, E = epandrium, P = proctiger; 29, female terminalia of *Proctacanthus micans* Schiner, lateral aspect.



Figs. 30–33. Utah Asilidae, lateral aspect of head and thorax: 30, *Scleropogon indistinctus* (Bromley) showing hairs on katatergite (hypopleuron); 31, *Stenopogon inquinatus* Loew showing bare katatergite (hypopleuron); 32, *Machimus occidentalis* (Hine) showing hairs on both katatergite and anatergite; 33, *Promachus albifacies* Williston showing hairs on katatergite and bare anatergite.

11(10). Mystax largely black; foretarsus of male yellowish .... *jemezi* Wilcox & Martin

— Mystax largely white, particularly above (some females with a few black hairs above); foretarsus of male black ...... *montanus* Loew

12(10). Foretarsus of male yellowish with white hairs; mystax of male white above ... *rufotarsus* Back

— Foretarsus of male black with black hairs; mystax all black ... *stenofrons* Wilcox & Martin

13(2). Pollinose fasciae of abdominal segment 1 entire or nearly so 14

— Pollinosity of abdominal segment 1 limited to patches near lateral margins, not extending medially across segment 16

14(13). Tibiae and femora reddish below; mystax black except for a few central, white hairs .. .. *profusus* Osten Sacken

— Tibiae and femora black, midtibia sometimes reddish in male; mystax white above, black below 15

15(14). Pollinosity of abdominal segments narrowly interrupted along dorsal midline .... *thompsoni* Cole

— Pollinosity of abdominal segments entire but with central spot on several segments lacking pollen .... *ablautoides* Melander

16(13). Scutellar hairs in large part white; pollinose fasciae of abdominal segments extending anteriorly along lateral margins .... *idahoensis* Wilcox & Martin

— Scutellar hairs all black, pollinose fasciae of abdominal segments not extending forward . ... *banksi* Wilcox & Martin

Key to the Species of Utah *Dioctria* Meigen

(Modified from Adisoemarto and Wood 1975)

1. Pleuron with golden pollinose band extending uninterrupted from between base of wing and humeral callus to coxa .... *vera* Back

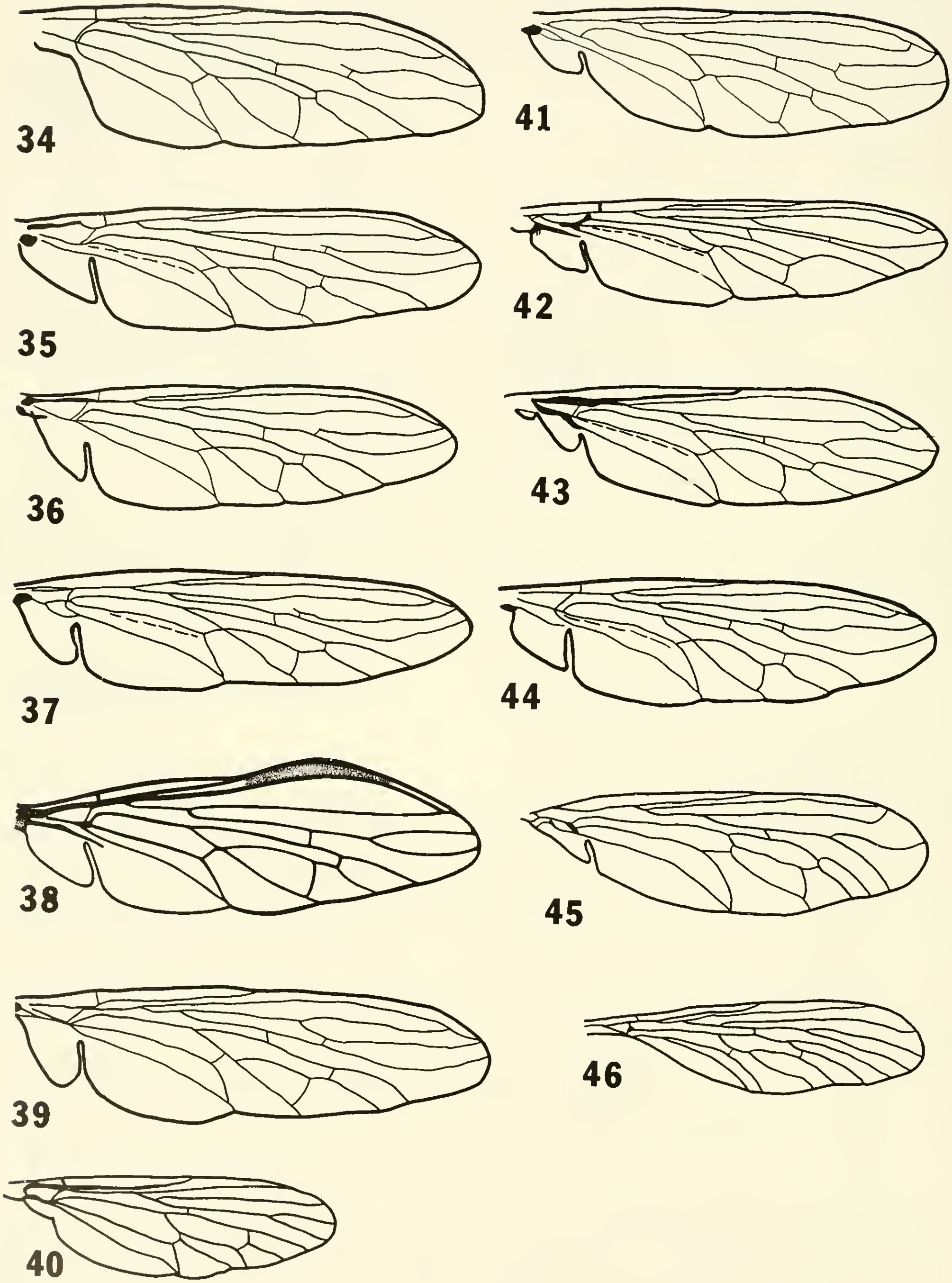
— Pleuron with discontinuous pollinose band, broadly interrupted on anterior margin of mesopleuron; interruption as wide as high 2

2(1). Pollinosity of mesopleuron restricted to and mostly covered by haired area near prothoracic spiracle .... *pusio* Osten Sacken

— Pollinosity of mesopleuron extending from prothoracic spiracle to base of wing .... *henshawi* Johnson

Key to the Species of Utah *Eucyrtopogon* Curran

The genus *Eucyrtopogon* Curran occurs in Utah with possibly as many as four or five species represented. The Curran (1923a) key easily distinguishes one species, *E. comantis* Curran, by the presence of a medial crest of white hairs on the mesonotum of the males. The other representatives of this genus in the state do not key out well. There are only eight



Figs. 34–46. Utah Asilidae, right wing: 34, *Efferia aestuans* (Linnaeus); 35, *Efferia albibarbis* (Macquart); 36, *Efferia apache* Wilcox; 37, *Efferia benedicti* (Bromley); 38, *Efferia costalis* (Williston); 39, *Efferia pernicus* Coquillett; 40, *Cyrtopogon willistoni* Curran; 41, *Efferia tucsoni* Wilcox; 42, *Promachus albifacies* Williston; 43, *Machimus occidentalis* (Hine); 44, *Efferia frewingi* Wilcox; 45, *Laphystia tolandi* Wilcox; 46, *Leptogaster* sp. from Clear Creek, Raft River Mountains, Box Elder Co., Utah.

specimens before me from the collections at BYU, UU, SUSC, and CEU. These specimens seem to represent three distinct species. The specimens from USU have been sent to R. Lavigne at the University of Wyoming, as he is at present studying the genus. Seven of the USU specimens are labeled *E. nebulo* as determined by Bromley; other specimens are simply labeled *Eucyrtopogon* sp. Any determination of the species in Utah (except *E. comantis*) would be very tenuous on my part, due to the small number of specimens which I have seen; thus, determinations of *Eucyrtopogon* from Utah must await the work which Lavigne is preparing.

Key to the Species of Utah *Heteropogon* Loew

(Modified from Wilcox 1965)

1. Scutellum without marginal bristles; wing with dark spots on crossveins and furcations . . . . . . *maculinervis* James

— Scutellum with marginal bristles; wings hyaline 2

2(1). Scutellum polished on hind margin, disc of scutellum pollinose; terminal abdominal segments red . . . . . . *stonei* Wilcox

— Scutellum entirely pollinose, sometimes thinly so, subshining black; terminal abdominal segments black 3

3(2). Black bristles of mystax extending greater than one-third distance from oral margin to antennae 4

— Black bristles of mystax confined to oral margin extending less than one-third distance from oral margin to antennae 5

4(3). Male with brush of black hairs in basal third of midtibia; hairs of mystax both black and white; scutellar bristles black . . . . . . *senilis* Bigot

— Males without brush of black hairs on midtibiae; hairs of mystax all white; scutellar bristles black . . . . . . species 1

5(3). Bristles of thorax and scutellum white, rarely one or two presutural black bristles; bristles of mystax black and white, white bristles above . . . . . . *martini* Wilcox

— Bristle of thorax both black and white; bristles of scutellum black; bristles of mystax all black . . . . . . *arizonensis* Wilcox

Key to the Species of Utah *Holopogon* Loew

(Modified from Martin 1959)

1. Mesonotum without presutural bristles laterally . . . . . . *caesariatus* Martin

— Mesonotum with two or more presutural bristles laterally 2

2(1). Scutellum lacking pollen on posterior portion of disc near margin . . . . . . *wilcoxi* Martin

— Scutellar disc pollinose (narrow margin may appear to be lacking pollen) 3

3(2). Scutellar disc lacking hair . . . . . . *currani* Martin

— Scutellar disc with a few to many hairs 4

4(3). Anterior mesonotal hairs sparse, erect, mostly brown . . . . . . *mingusae* Martin

— Anterior mesonotal hairs dense, somewhat recumbent, white . . . . . . *albipilosus* Curran

Key to the Species of Utah *Laphystia* Loew

(Modified from Wilcox 1960)

1. Scutellum with marginal bristles nearly as strong as lateral bristles of mesonotum; femora mostly dark brown, apices yellowish . . . . . . *tolandi* Wilcox

— Scutellum with marginal hairs weak and procumbent or absent; femora usually concolorous . 2

2(1). Marginal scutellar hairs weak and procumbent; abdomen not reddish 3

— Marginal scutellar hairs absent; abdomen reddish brown . . . . . . *rubra* Hull

3(2). Abdomen yellowish, fasciae on segments 3–5 one-third length of segments; femora of both sexes wholly reddish; pollen of abdominal fasciae white . . . . . . *utahensis* Wilcox

— Abdomen brown, femora yellowish, pollen of abdominal fasciae yellow . . . . . . *annulata* Hull

Key to the Species of Utah *Lasiopogon* Loew

(Modified from Cole and Wilcox 1938)

1. Marginal scutellar bristles white . . . . . . *albidus* Cole & Wilcox

— Marginal scutellar bristles black 2

2(1). Surstyli of male genitalia one and one-third times as long as high in lateral view (Fig. 12); male genitalia wider than adjacent abdominal segment in dorsal view (Fig. 13); sternite 9 of female genitalia amber colored . . . . . . *aldrichii* Melander

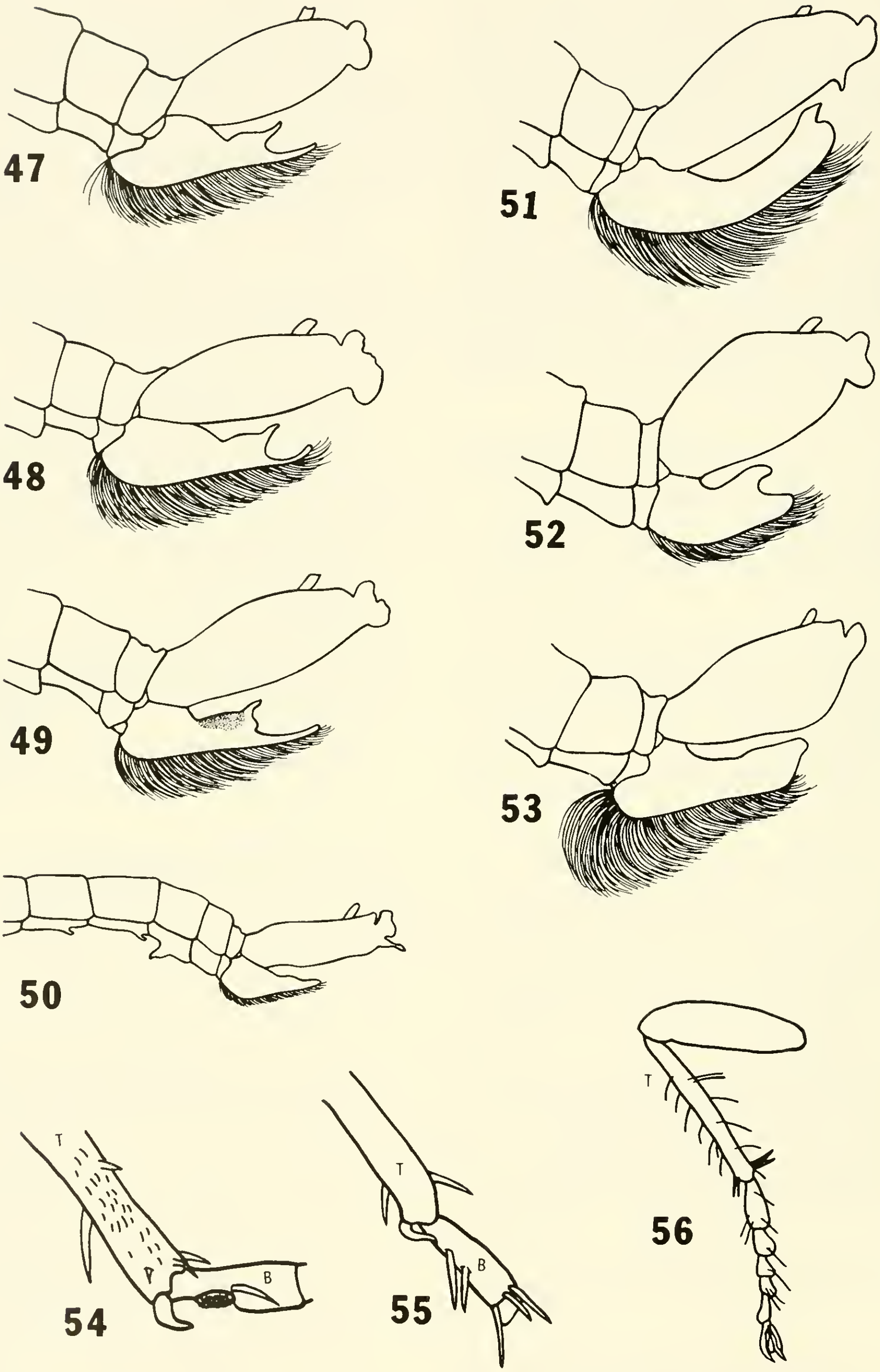
— Surstyli of male about two or more times as long as high in lateral view (Fig. 14), male genitalia narrower than abdomen in dorsal view; sternite 9 of female genitalia dark brown or black 3

3(2). Surstyli of male covered with ash-colored pollen; surstyli without tooth on ventral margin before base (Fig. 16) (Note: male genitalia may be rotated 180 degrees) . . . . . . *cinereus* Cole

— Surstyli of male shining black or brown, surstyli with prominent tooth on ventral margin near base (Fig. 15) . . . . . . *monticola* Melander

Key to the Species of Utah *Nicocles* Jaennicke

(Modified from Wilcox 1946)



Figs. 47–56. Utah Asilidae, lateral aspect of male terminalia and legs: 47, male terminalia of *Efferia utahensis* (Bromley); 48, male terminalia of *Efferia frewingi* Wilcox; 49, male terminalia of *Efferia mortensoni* Wilcox; 50, male terminalia of *Efferia tucsoni* Wilcox; 51, male terminalia of *Efferia bicolor* (Bellardi); 52, male terminalia of *Efferia albibarbis* (Macquart); 53, male terminalia of *Efferia zonata* (Hine); 54, foretibia and basitarsus of *Diogmites grossus* Bromley, B = basitarsus, T = tibia; 55, foretibia and basitarsus of *Cophura scitula* Williston, B = basitarsus, T = tibia; 56, middle leg of *Callinicus pollenius* (Cole), T = tibia.

1. Abdominal segments 3–7 of male and 4–6 of female red, silver fasciae covering entire dorsum of male segments 5–6 .... *abdominalis* Williston

— All abdominal segments of male and female black; silver fasciae of male covering entire dorsum of segment 6 and basal portion of segment 5 .... *utahensis* Banks

Key to the Species of Utah *Ospriocerus* Loew

(Modified from Martin 1968)

1. Abdominal segments entirely black .... *minos* Osten Sacken

— Abdominal segments in part reddish, or brown pollinose 2

2(1). Abdominal segments brown pollinose, tan in ground color .... *longulus* (Loew)

— Abdominal segments in part red, not pollinose . 3

3(2). Tip of flagellum with notch containing small inconspicuous spine (Fig. 8) ..... *abdominalis* (Say)

— Tip of flagellum produced as apical segment (Fig. 9) .... *vallensis* Martin

Key to the Species of Utah *Scleropogon* Loew

(Modified from Wilcox 1971)

1. Cells r_5 and m_3 with long petioles subequal to length of rm crossvein .... *picticornis* Loew

— Cells r_5 and m_3 either open or with one or other having a short petiole 2

2(1). Antennal segment 3 one and three-fourth times as long as segments 1–2; abdomen slender, gray pollinose; wings tinged with brown .... *duncani* (Bromley)

— Antennal segment 3 at most one and one-half times as long as segments 1–2; abdomen stockier; wings hyaline 3

3(2). Hypopleuron with bristles, cell m_3 closed and usually short petiolate 4

— Hypopleuron with hairs, cell m_3 broadly open . . 5

4(3). Abdomen stout, apex of wings reaching to tergite 6; ground color of most of abdomen tan; length 15–19 mm .... *coyote* (Bromley)

— Abdomen elongate, apex of wings not reaching to tergite 6 but covering base of tergite 5; ground color of abdomen dark brown with bases and apices of segments tan; length 19–26 mm .... *indistinctus* (Bromley)

5(3). Abdomen black, narrow posterior and lateral margins of tergites tan; densely pollinose .... *neglectus* (Bromley)

— Abdomen reddish brown, black laterally on basal segments; thinly pollinose .... *bradleyi* (Bromley)

Key to the Species of Utah *Stenopogon* Loew

(Modified from Wilcox 1971)

1. Gibbosity of face extending about one-half to three-fourths distance from oral margin to antennae (Fig. 3); fore coxae with numerous bristles 2

— Gibbosity extending about five-sixths to seven-eighths distance from oral margin to antennae (Fig. 2); fore coxae with numerous long hairs . . . 3

2(1). Gibbosity weak, face not strongly inflated; shiny black triangle between mystax and antennae absent; small, length 9–10 mm . . *utahensis* Bromley

— Gibbosity strong, face strongly inflated; shiny black triangle between mystax present; large, length 20–37 mm .... *inquinatus* Loew

3(1). Abdomen densely pollinose; long hairs on inner arms of hypandrium continuing across base . . . . *martini* Bromley

— Abdomen subshining black; long hairs on inner arms of hypandrium interrupted medially 4

4(3). Hind tibiae with indistinct reddish area at least near apex; mystax yellowish .... *engelhardti* Bromley[3]

— Hind tibiae all reddish or yellowish, mystax reddish .... *rufibarbis* Bromley[3]

Key to the Utah *Stichopogon* Loew

(Modified from Wilcox 1936b)

1. Scutellum with marginal hairs or bristles; pollen of abdomen golden and brown; length 3–5 mm .... *fragilis* Back

— Scutellum lacking marginal hairs or bristles; pollen of abdomen silver; length greater than 6 mm 2

2(1). Tergite 4 mostly silvery pollinose sometimes with medial portion of apex lacking pollen .... *trifasciatus* Say

— Tergite 4 with black band covering basal third . ... *salinus* (Melander)

Key to the Genera of Utah Laphriinae

1. Postmetacoxal area forming a sclerotized arch when viewed from below; flagellum bearing either a short dorsal bristle or terminal style 2

— Postmetacoxal area entirely membranous; flagellum without dorsal bristle or terminal style, apical pit may contain a short bristle 3

2(1). Coloration and pile resembling a bumblebee; anatergite bare; length over 25 mm .... *Dasyllechia atrox* (Williston)

— Body quite bare, not resembling a bumblebee; anatergite haired or with bristles; length less than 20 mm ..... *Atomosia mucida* Osten Sacken

3(1). Proboscis compressed laterally; some species resembling bumblebees in pile and coloration .... *Laphria* Meigen

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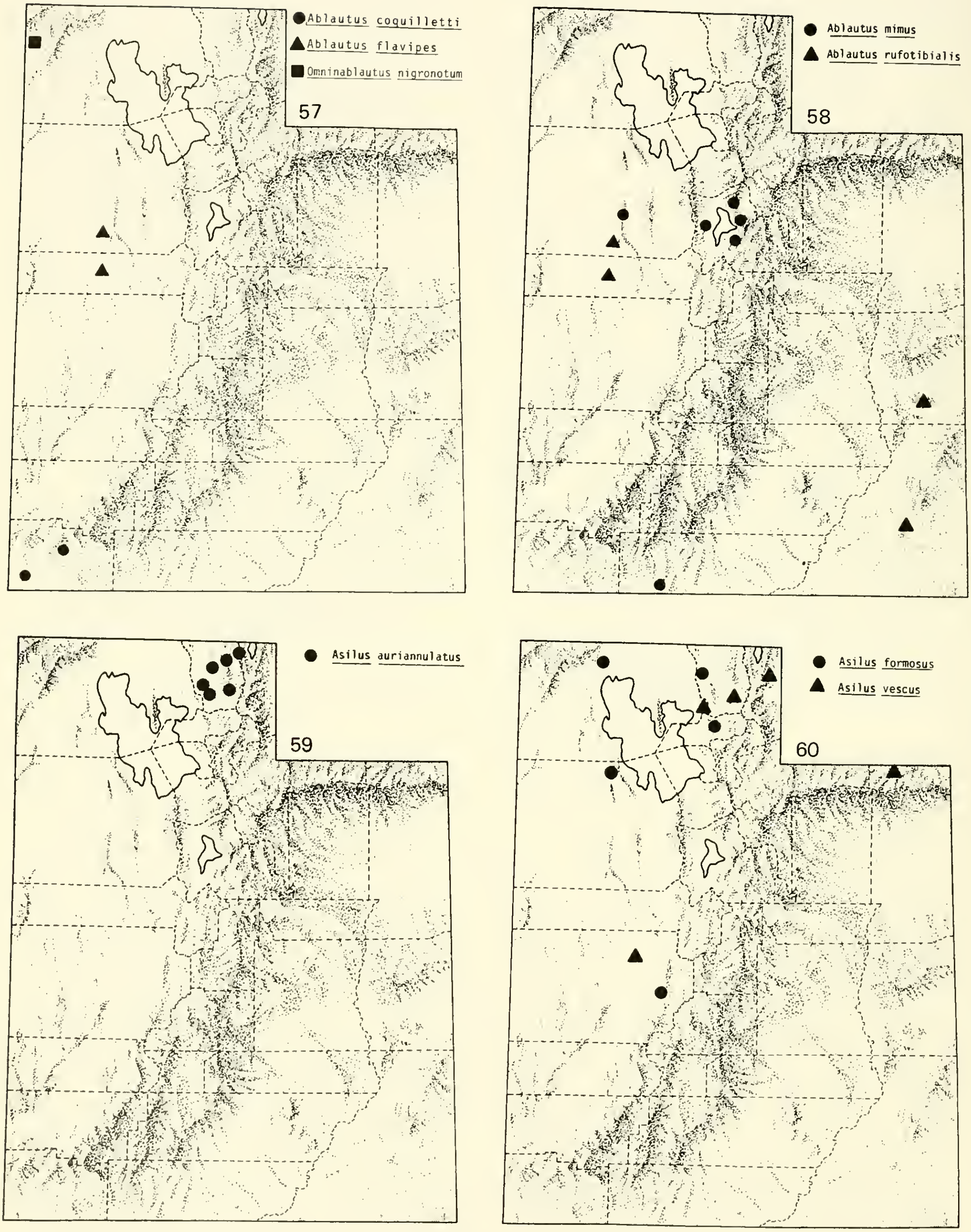
[3] Wilcox has determined specimens as being either *S. engelhardti* or *S. rufibarbis* from the same localities which do not agree with the final couplet of this key. It may be that the characters used in this key (adapted from Wilcox 1971) are not dependable in separating Utah specimens of these two species.


● Ablautus coquilletti
▲ Ablautus flavipes
■ Omninablautus nigronotum
57
● Ablautus mimus
▲ Ablautus rufotibialis
58
● Asilus auriannulatus
59
● Asilus formosus
▲ Asilus vescus
60

Figs. 57–60. Utah Asilidae, distribution: 57, *Ablautus coquilletti*, *Ablautus flavipes*, and *Omninablautus nigronotum*; 58, *Ablautus mimus* and *Ablautus rufotibialis*; 59, *Asilus auriannulatus*; 60, *Asilus formosus* and *Asilus vescus*.

— Proboscis flattened dorsoventrally; abdomen mostly bare and reddish orange . . . . *Cerotainiops abdominalis* (Brown)

Key to the Genera and Species of Utah Asilinae

(Modified from Wood 1981)

1. Anatergite (metanotal callus) bare (Fig. 33) . . 2

— Anatergite (metanotal callus) with bristles or hairs (Fig. 32) 9

2(1). R_4 with recurrent vein; recurrent branch (stump vein) sometimes short (Fig. 35), ending in cell r_{2+3} or extending basally and joining R_{2+3} (Fig. 42) 3

— R_4 without recurrent vein (Fig. 43) 7

3(2). Cell r_4 narrow, apical half of R_5 subparallel with R_4 (Figs. 35–39) . . . . . . *Efferia* Coquillett

— Cell r_4 broad, apical half of R_5 diverging strongly from R_4 (Fig. 42) 4

4(3). Claws acute; abdomen elongate 6

— Claws blunt; abdomen stout 5

5(4). Lower face inflated; hind femur club-shaped, with row of bristles below near apex; Utah specimens have black pile on thorax . . . . *Mallophora fautrix* Osten Sacken

— Lower face not greatly inflated; hind femur spindle-shaped and without bristles below near apex; pile of thorax in Utah specimens mostly gray and/or yellow . . . *Megaphorus* Bigot

6(4). Recurrent branch (stump vein) short (similar to *Efferia*), not reaching R_{2+3} . . . . *Triorla interrupta* Macquart

— Recurrent vein extending to and connecting with R_{2+3} . . . . *Promachus* Loew

7(2). R_5 reaching wing margin anterior to apex of wing . . . . *Proctacanthus* Macquart

— R_5 reaching wing margin posterior to apex of wing 8

8(7). Epandria of male black and elongate, longer than tergite 6; terminalia of females lacking strong bristles . . . . *Regasilus blantoni* Curran

— Epandria of male red and short, subequal to length of tergite 6 (Fig. 22); terminalia of female bearing strong bristles (Fig. 23) . . . . *Proctacanthella cacopiloga* Bromley

9(1). Occipital bristles long and fine, distal third strongly bent anteriad at nearly a 90 degree angle (Fig. 5) . . . *Neoitamus brevicomus* (Hine)

— Occipital bristles stout, not bent forward at a sharp angle, but may bend forward gradually throughout length 10

10(9). Epandria of male arching to enclose an open space when viewed from above (Fig. 18); terminalia of female bearing several pairs of stout bristles (Fig. 19) . . . . *Philonicus* Loew

— Epandria of male not arching to enclose an open space when viewed from above, but touching along most of dorsomedial margin (Fig. 20); terminalia of female lacking stout bristles (Fig. 21) 11

11(10). Length of antennal style at least one and one-third length of antennal segment 3; inner surface of epandrium of male with patch of erect spines . . . . *Polacantha* Martin

— Length of antennal style of antenna shorter than or subequal to length of antennal segment 3; inner surface of epandrium lacking erect spines 12

12(11). Epandria of male notched near apex (Fig. 11) . . . . *Neomochtherus* Osten Sacken

— Epandria of male not notched near apex (Fig. 24) 13

13(12). Style about one-fourth length of antennal segment 3; bristles of tergites 2 and 3 short and recumbent . . . . *Negasilus* Curran

— Style longer than one-fourth length of antennal segment 3; bristles of tergites 2 and 3 longer and erect 14

14(13). Epandria of males pointed and directed upward at apex (Fig. 17), apices diverging . . . . *Asilus auriannulatus* Hine

— Epandria of males not pointed and not directed upward at apex, apices converging . . . . . *Machimus* Loew, *Asilus vescus* Hine, and *A. formosus* Hine

Key to the Species of Utah *Efferia* Coquillett

(Modified from Wilcox 1966a)

1. Three submarginal cells in wings (no vein ending in a submarginal cell, but continuing to meet R_2), (Fig. 39)(Anomala group) 2

— Two submarginal cells in wings, 'stump' vein present and ending in first submarginal cell . . 3

2(1). Hairs on abdominal sternites much longer than antennal segments 1–2 combined . . . . *pernicus* Coquillett

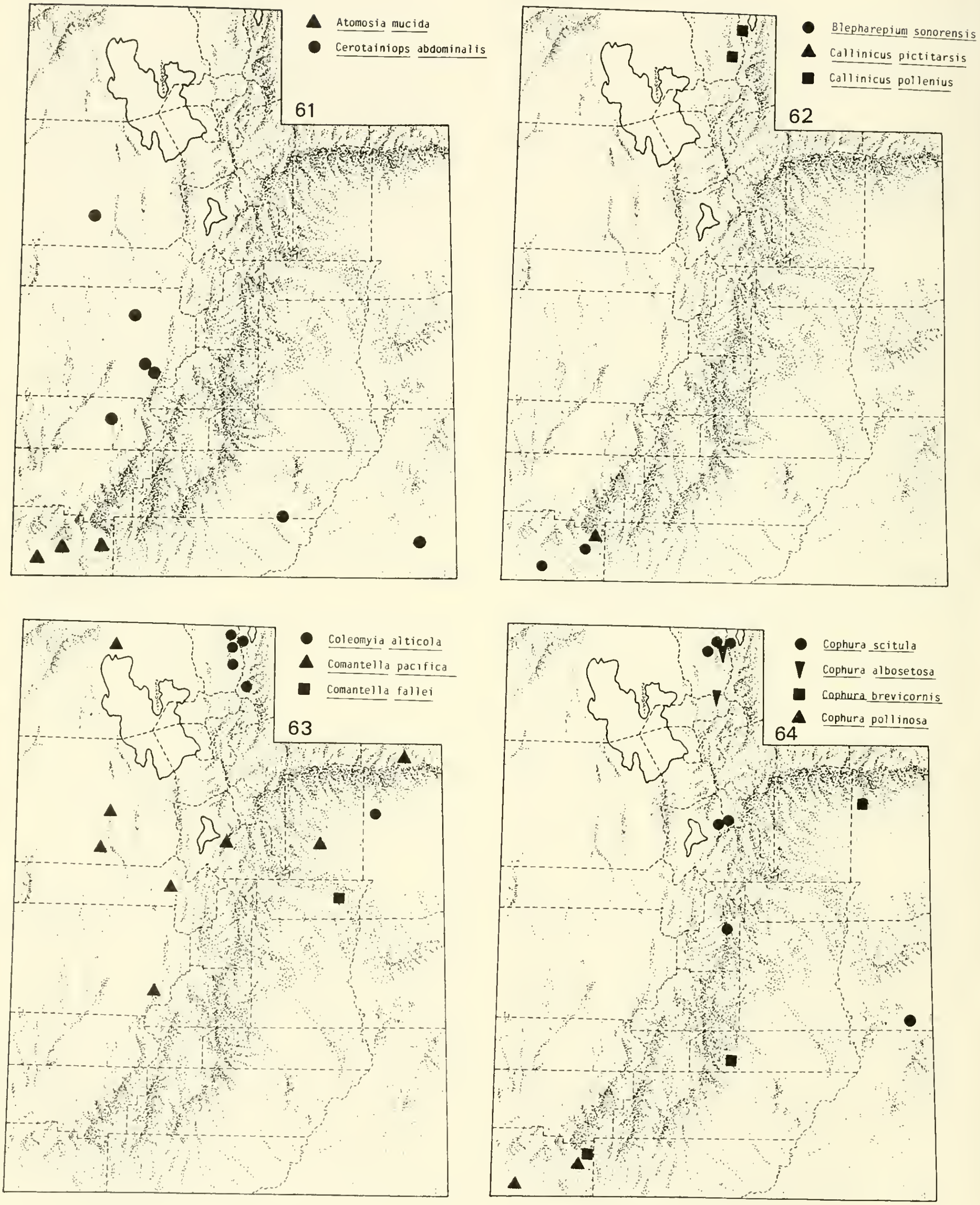
— Hairs on abdominal sternites subequal to antennal segment 1 in length . . . . . . *davisi* Wilcox

3(1). R_{4+5} forking before apex of discal cell (Figs 37, 44) 4

— R_{4+5} forking at or beyond apex of discal cell (Figs. 34–36, 38, 41) 11

4(3). Mesonotum anteriorly with bristles or hairs at least as long as antennal segments 1–2 combined; color of male abdominal segments 2–5 alternating black and white; lacking long parted hairs; segment 6–7 white pollinose; ovipositor pointed and split at tip when viewed from above (Pogonias group) 5

— Mesonotum anteriorly with bristles and hairs shorter than antennal segments 1–2 combined; color of male abdominal segments gray or white pollinose, often with white parted hairs; ovipositor rounded at tip, not split when viewed from above (Staminea group) . . 7


▲ Atomosia mucida
● Cerotainiops abdominalis
61
● Blepharepium sonorensis
▲ Callinicus pictitarsis
■ Callinicus pollenius
62
● Coleomyia alticola
▲ Comantella pacifica
■ Comantella fallei
63
● Cophura scitula
▼ Cophura albosetosa
■ Cophura brevicornis
▲ Cophura pollinosa
64

Figs. 61–64. Utah Asilidae, distribution: 61, *Atomosia mucida* and *Cerotainiops abdominalis*; 62, *Blepharepium sonorensis*, *Callinicus pictitarsis*, and *Callinicus pollenius*; 63, *Coleomyia alticola*, *Comantella pacifica*, and *Comantella fallei*; 64, *Cophura scitula*, *Cophura albosetosa*, *Cophura brevicornis*, and *Cophura pollinosa*.

5(4). Lower forceps of male with apical lobes forming an acute angle when viewed laterally (Fig. 47); scutellar bristles and hairs white (sometimes one black); mystax with at most four black bristles; females with fore and middle tibiae black, sometimes brownish dorsally near bases .... *utahensis* (Bromley)

— Lower forceps of male with apical lobes meeting basally as a broad U or with a flattened area between them at base (Figs. 48–49); scutellum with black bristles and white hairs or white bristles and black hairs, bristles and hairs not all white; mystax with at least eight black hairs or bristles along oral margin; females usually with fore and middle tibiae brown, if black then scutellar bristles black .. 6

6(5). Lower forceps of male with apical lobes joining in a broad, evenly curved U when viewed laterally (Fig. 48); scutellar bristles usually black (at least in part), hairs of scutellum usually white; common .... *frewingi* Wilcox

— Lower forceps of male with a broad relatively flat area between the apical lobes (Fig. 49); scutellar bristles white (at most one black), hairs of scutellum all black; rare, single specimen from St. George ...... *mortensoni* Wilcox

7(4). Mystax yellow, pollen of face yellow (slightly yellow in female but contrasting with white hairs of postgena) .... *staminea* (Williston)

— Mystax and pollen of face silvery white, hairs of mystax and postgena both white 8

8(7). Sternite 8 of male produced medially at apex; female with R$_{4+5}$ forking at or before middle of the distance between rm and apex of discal cell 9

— Sternite 8 of male not produced medially, straight when viewed from below; female with R$_{4+5}$ forking beyond middle of distance between rm and apex of discal cell 10

9(8). Anterior mesonotal crest shorter than antennal segment 1; sparse, white parted hairs on abdominal segments 2–4; abdomen grayish pollinose .... *benedicti* (Bromley)

— Anterior mesonotal crest subequal to length of antennal segments 1 and 2; long, white parted hairs on abdominal segments 2–5 and short parted on 6–7; abdomen silvery-white pollinose .... *basini* Wilcox

10(8). Fringe of hairs on surstyli of male white; white parted abdominal hairs long and dense on segments 1–7 of male; female indistinguishable from that of *cana* .... *deserti* Wilcox

— Fringe of hairs on lower forceps of male black in part; white parted abdominal hairs long on segments 1–4, short on segments 5–7, sparse on all; female indistinguishable from that of *deserti* .... *cana* (Hine)

11(3). R$_5$ reaching costa before apex of wing (Figs. 35–38, 41) 12

— R$_5$ reaching costa after apex of wing (Fig. 34) .... *aestuans* (Linnaeus)

12(11). Anterior part of mesonotum compressed laterally; acrostical crest of long hairs or bristles present (Carinata group) 13

— Anterior part of mesonotum not compressed laterally; crest, if present, extends onto dorsocentral row as well as acrostical row 15

13(12). Abdomen of male lacking long, white parted hairs; black of segments 2–4 extensive; mesonotal crest short, subequal to antennal segment 1; ovipositor greater than 4 mm in length .... *willistoni* (Hine)

— Abdomen of male with long, white parted hairs; black of segment 2–4 limited (at most) to hind margins; mesonotal crest subequal to length of antennal segments 1–3; ovipositor usually less than 4 mm in length (if longer, then mesonotal crest long) 14

14(13). Abdominal segment 7 of male with mostly black hairs; ovipositor about 4 mm long .... *subcuprea* (Schaeffer)

— Abdominal segment 7 of male with mostly white hairs; ovipositor 3.5 mm or less in length (wing, Fig. 38) ...... *costalis* (Williston)

15(12). Mesonotum anteriorly with numerous erect hairs or bristles as long as antennal segments 1–3; marginal bristles of scutellum numerous; bristles of tarsi mostly white (Arida group) .. 16

— Mesonotum anteriorly with bristles and hairs shorter than antennal segments 1–2; fewer than ten marginal scutellar bristles 18

16(15). Mystax mostly white, 1–8 black hairs below and laterally; discal hairs of scutellum mostly white (especially in female); bristles and hairs of postalar callus mostly white (or a few of weaker bristles and hairs black) . *apache* Wilcox

— Mystax with dense black hairs below and laterally in male, lateral black hairs sparser in female but more than eight present; white hairs of scutellum limited to base and sides (or absent); bristles and hairs of postalar callus mostly black (with at least one strong white bristle) 17

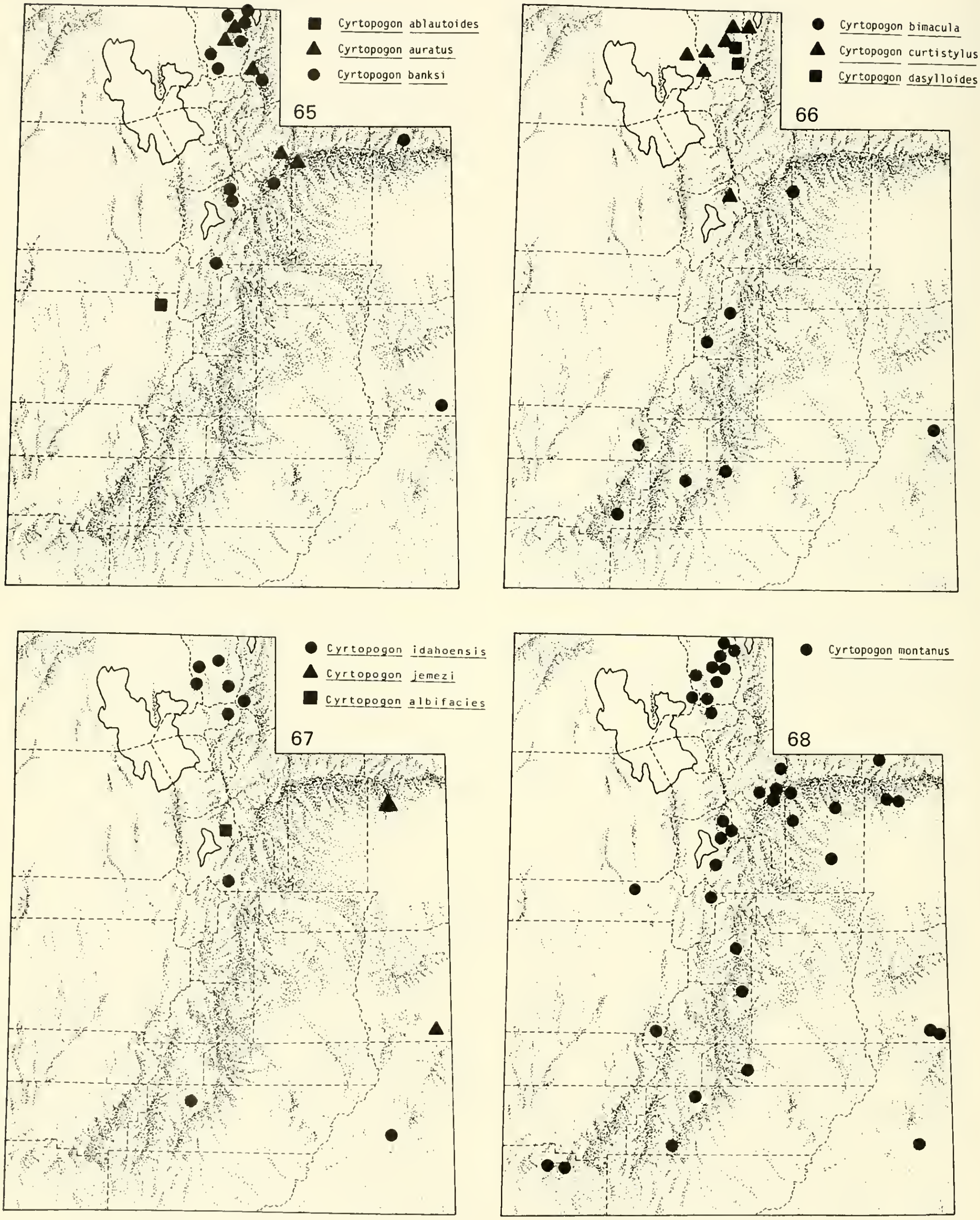
17(16). Foretibia mostly black, somewhat lighter basally; scutellar bristles black in male, white in female .... *arida* (Williston)

— Foretibia reddish basally and black apically; scutellar bristles white (only male seen; may simply be variant of *arida*) . *subarida* (Bromley)

18(15). Males with prominent, ventral tubercles on abdominal segments 4–7 (Fig. 50), slender species (Tuberculata group) 19

— Males without prominent tubercles on abdominal segments (Fig. 52); usually larger, stouter species (Albibarbis group) 20

19(18). Male terminalia and tubercles reddish; female abdominal segment 7 and base of ovipositor reddish; abdominal tergites largely white haired, some hairs of tergite 7 black .... *tucsoni* Wilcox


■ Cyrtopogon ablautoides
▲ Cyrtopogon auratus
● Cyrtopogon banksi
65
● Cyrtopogon bimacula
▲ Cyrtopogon curtistylus
■ Cyrtopogon dasylloides
66
● Cyrtopogon idahoensis
▲ Cyrtopogon jemezi
■ Cyrtopogon albifacies
67
● Cyrtopogon montanus
68

Figs. 65–68. Utah Asilidae, distribution: 65, *Cyrtopogon ablautoides*, *Cyrtopogon auratus*, and *Cyrtopogon banksi*; 66, *Cyrtopogon bimacula*, *Cyrtopogon curtistylus*, and *Cyrtopogon dasylloides*; 67, *Cyrtopogon idahoensis*, *Cyrtopogon jemezi*, and *Cyrtopogon albifacies*; 68, *Cyrtopogon montanus*.

— Male terminalia and tubercles black; female abdominal segment 7 and base of ovipositor black; abdominal tergites broadly black haired . . . . *producta* (Hine)

20(18). Male terminalia black; surstyli with ventral tooth near apex (Fig. 51); marginal scutellar bristles black with discal hairs long and white . . . . *bicolor* Bellardi

— Male terminalia reddish; surstyli without ventral tooth near apex (Figs. 52, 53); scutellum with either black bristles and some short black hairs or with bristles and hairs both white 21

21(20). Mystax all white; transverse black (or brownish) bands of abdomen interrupted by longitudinal lighter stripe; length of ovipositor subequal to length of abdominal segments 6–7; male genitalia as in Fig. 52 . . . . *albibarbis* (Macquart)

— Mystax black and white; transverse black bands of abdomen uninterrupted; length of ovipositor greater than length of abdominal segments 6–7; male genitalia as in Fig. 53 . . . . *zonata* (Hine)

Key to the Species of Utah *Machimus* Loew Including *Asilus formosus* Hine and *Asilus vescus* Hine

(Modified from Hine 1909 and Martin 1975)

1. Hind femur longitudinally yellowish brown on ventral surface and black on dorsal surface 2

— Hind femur with yellowish brown confined to apex, or hind femora entirely black 4

2(1). Wing with some dark coloration; especially near apex 3

— Wing entirely hyaline . . . . . *Asilus formosus* Hine

3(2). Wing with dark spots in medial cells; distal fourth of wing with dark coloration isolated from veins except at extreme tips; proctiger without ventral process near apex . . . . *griseus* (Hine)

— Wing without dark spots in medial cells, distal fourth of wing with faint dark wash reaching veins before apex; proctiger with ventral process near apex (Fig. 25) . . . . *adustus* Martin

4(1). Sternite 8 of male produced apically and bearing tuft of longer hairs on apex of produced area (Fig. 6) 5

— Sternite 8 of male not produced apically, hairs of uniform length across posterior margin (Fig. 7) . 6

5(4). Proctiger with two processes near its attachment to abdomen; medial areas of tergites covered with brown pollen . . . . *sestertius* Martin

— Proctiger lacking processes; medial areas of tergites covered with dense, silvery pollen . . . . *occidentalis* (Hine)

6(4). Small, less than 11 mm in total length; male terminalia reddish brown . . . . . *Asilus vescus* Hine

— Larger, greater than 12 mm in total length; male terminalia black or dark brown 7

7(6). Pollen of abdomen golden; color of incisures not contrasting greatly with color of remainder of each segment . . . . *paropus* (Walker)

— Pollen of abdomen silvery; incisures yellowish, contrasting with the black remainder of each segment . . . . *callidus* (Williston)

Key to the Species of Utah *Megaphorus* Bigot

(Modified from Cole and Pritchard 1964)

1. Costa ending near wing tip 2

— Costa continuing around wing tip to hind margin 4

2(1). Cell r_5 open . . . . *pulcher* (Pritchard)

— Cell r_5 closed, usually petiolate 3

3(2). Wing veins brown . . . . *willistoni* (Cole)[4]

— Wing veins yellow . . . . *guildiana* (Williston)[4]

4(1). Pile of thorax and abdomen white, wings yellowish; length 10 mm . . . . *pallidus* (Johnson)

— Pile of thorax and abdomen bright yellow, wings brownish; length 12–14 mm . . *frustra* (Pritchard)

Key to the Species of Utah *Negasilus* Curran

1. Margin of scutellum with bristles . . . *mesae* (Tucker)

— Margin of scutellum lacking bristles . . . *belli* Curran

Key to the Species of Utah *Neomochtherus* Osten Sacken

1. Face white, disc of scutellum lacking long, white hairs . . . . *hypopygialis* (Shaeffer)

— Face brown; disc of scutellum with long, white hairs 2

2(1). Wings of male with brown color concentrated in area near middle of anterior half of wing; anal lobe of male hyaline . . . . *lepidus* (Hine)

— Wings of male with brown color evenly distributed throughout; anal lobe of male tinged with brown . . . . *albicornis* (Hine)

Key to the Species of Utah *Philonicus* Loew

1. Wing smoky; legs dark red . . *arizonensis* (Williston)[5]

— Wing clear; legs pale reddish . *limpidipennis* (Hine)[5]

Key to the Species of Utah *Proctacanthus* Macquart

(Modified from Hine 1911)

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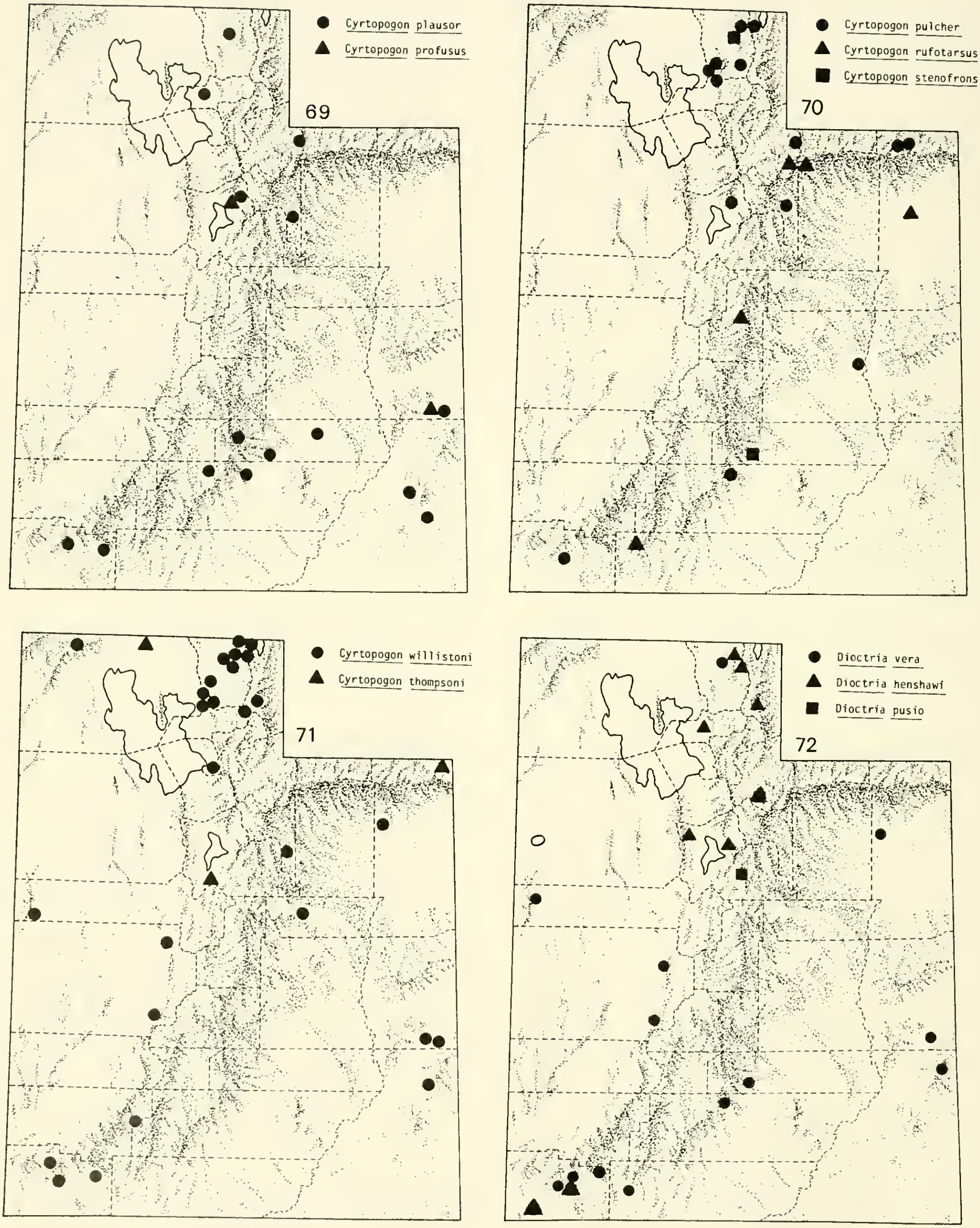
[4] With regard to *M. willistoni* and *M guildiana*, Cole and Pritchard state, "Some populations [of *willistoni*], particularly in Utah, tend to blend with *guildiana*." After examining the specimens of these species found in the state, I found the key lead most comfortably to *willistoni*.

[5] Specimens of both species have been identified by Bromley and Wilcox as occurring scattered throughout the state. Using the above key derived from Hine (1909) and Bromley (1934), I found that specimens from Utah seem to run best to *arizonensis*.


● Cyrtopogon plausor
▲ Cyrtopogon profusus
69
● Cyrtopogon pulcher
▲ Cyrtopogon rufotarsus
■ Cyrtopogon stenofrons
70
● Cyrtopogon willistoni
▲ Cyrtopogon thompsoni
71
● Dioctria vera
▲ Dioctria henshawi
■ Dioctria pusio
72

Figs. 69–72. Utah Asilidae, distribution: 69, *Cyrtopogon plausor* and *Cyrtopogon profusus*; 70, *Cyrtopogon pulcher*, *Cyrtopogon rufotarsus*, and *Cyrtopogon stenofrons*; 71, *Cyrtopogon willistoni* and *Cyrtopogon thompsoni*; 72, *Dioctria vera*, *Dioctria henshawi*, and *Dioctria pusio*.

1. Body with ground color reddish orange . . . . *hinei* Bromley

— Body with ground color black and orange 2

2. Wings with uniform brownish tinge[6] . . . . *milberti* Macquart

— Wings clear or with brown concentrated near veins 3

3(2). Epandria of male genitalia curving outward and then back to enclose a space between tips and proctiger when viewed from above (Fig. 26); terminal keellike sternite of female lacking strong spines ventrally (Fig. 27); circlet of spines present dorsally . . . . *nearno* Martin

— Epandria not enclosing a space, but straight and compact against proctiger (Fig. 28); terminalia of female with ventral keellike projection covered with stout spines in addition to dorsal circlet of spines (Fig. 29) . . . . *micans* Schiner

Key to the Species of Utah *Promachus* Loew

(Modified from Hine 1911)

1. First submarginal cell with dark, distinct gray cloud 2

— First submarginal cell clear or with very faint, narrow gray line; black areas of abdomen with few to many white hairs near lateral and posterior margins of segments . . . . *aldrichii* Hine

2(1). Male genitalia without silvery hairs above; tibiae yellow in contrast to black femora . . *sackeni* Hine

— Male genitalia with silvery hairs above; tibiae and femora more or less concolorous, not contrasting greatly 3

3(2). Mystax white, sometimes slightly yellow; thorax gray pollinose; male abdominal tergite 3 without lateral patch of dense black hairs; light hairs of abdomen whitish gray . . . . *albifacies* Williston

— Mystax yellowish; thorax brownish yellow pollinose; male abdominal tergite 3 with lateral patch of dense black hairs; light hairs of abdomen yellowish . . . . *dimidiatus* Hine

SYNOPSIS OF SPECIES

Subfamily Dasypogoninae

Ablautus coquilletti **Wilcox** 1935: 226 [Holotype: male, Los Angeles Co., California in USNM]. Utah distribution: Washington Co.: Leeds Cyn., Santa Clara. 4 May–2 June.

Ablautus flavipes **Coquillett** 1904: 178 [Types: Three males and two females, Los Angeles and San Diego counties, California in USNM]. Utah distribution: Juab Co.: Topaz Mtn.; Tooele Co.: Dugway Proving Ground. 26 April–20 June.

Ablautus mimus **Osten Sacken** 1877: 290 [Holotype: male, Crafton near San Bernardino, California, March in MCZ]. Utah distribution: Carbon Co.: Woodhill; Emery Co.: Elmo; Kane Co.: Kanab; Tooele Co.: Cedar Mtns.; Utah Co.: Alpine, Provo, Spanish Fork, Vineyard (now Geneva Steel), west side Utah Lake. 6 April–4 July.

Ablautus rufotibialis **Back** 1909: 182 [Holotype: female, Ysleta, Texas, 2 April 1902 in AESP]. Utah distribution: Grand Co.: Moab; Juab Co.: Topaz Mtn.; San Juan Co.: Comb Wash 32 mi SW Blanding; Tooele Co.: Dugway Proving Ground. 17–22 April.

Blepharepium sonorensis **Papavero and Bernardi** 1973: 175 [Holotype: Arizona, Palos Verdes, viii. 1949, in Museu Zoologia da Universidade de Sao Paulo]. Utah distribution: Washington Co.: St. George, Coalpits Wash, Zion National Park. 5–18 August.

Bohartia **sp.** Utah distribution: Rich Co.: Dry Basin. 4 August.

Callinicus pictitarsis **(Bigot)** 1878: 411 [Holotype: California; in Bigot Collection]. Utah distribution: Washington Co.: Zion National Park. No dates on labels.

Callinicus pollenius **(Cole)** in Cole and Lovett, 1919: 237 [Holotype: male, Hood River, Oregon, 24 September 1917; #491 in CAS]. Utah distribution: Cache Co.: Blacksmith Fork Canyon; Rich Co.: Logan Canyon summit. 30 July–1 September.

Coleomyia alticola **James** 1941: 37 [Holotype: male, Science Lodge near Ward, Colorado, 24 July 1939, repository not listed]. Utah distribution: Cache Co.: Beaver Mountain, Blacksmith Fork Canyon, Tony Grove; Rich Co.: Logan Canyon summit, Monte Cristo; Uintah Co.: Whiterocks. 6 June–14 August.

Comantella fallei **(Back)** 1909: 278 [Lectotype: male, Fort Collins, Colorado, 30 March 1900; in CSU]. Utah distribution: Carbon Co.: Sunnyside. 11-10-1936.

Comantella pacifica **Curran** 1926: 311 [Holotype: Penticton, B.C., 4 April 1919, #2320 in CNC]. Utah distribution: Box Elder Co.: Wildcat Hills; Carbon Co.: Price Airport;

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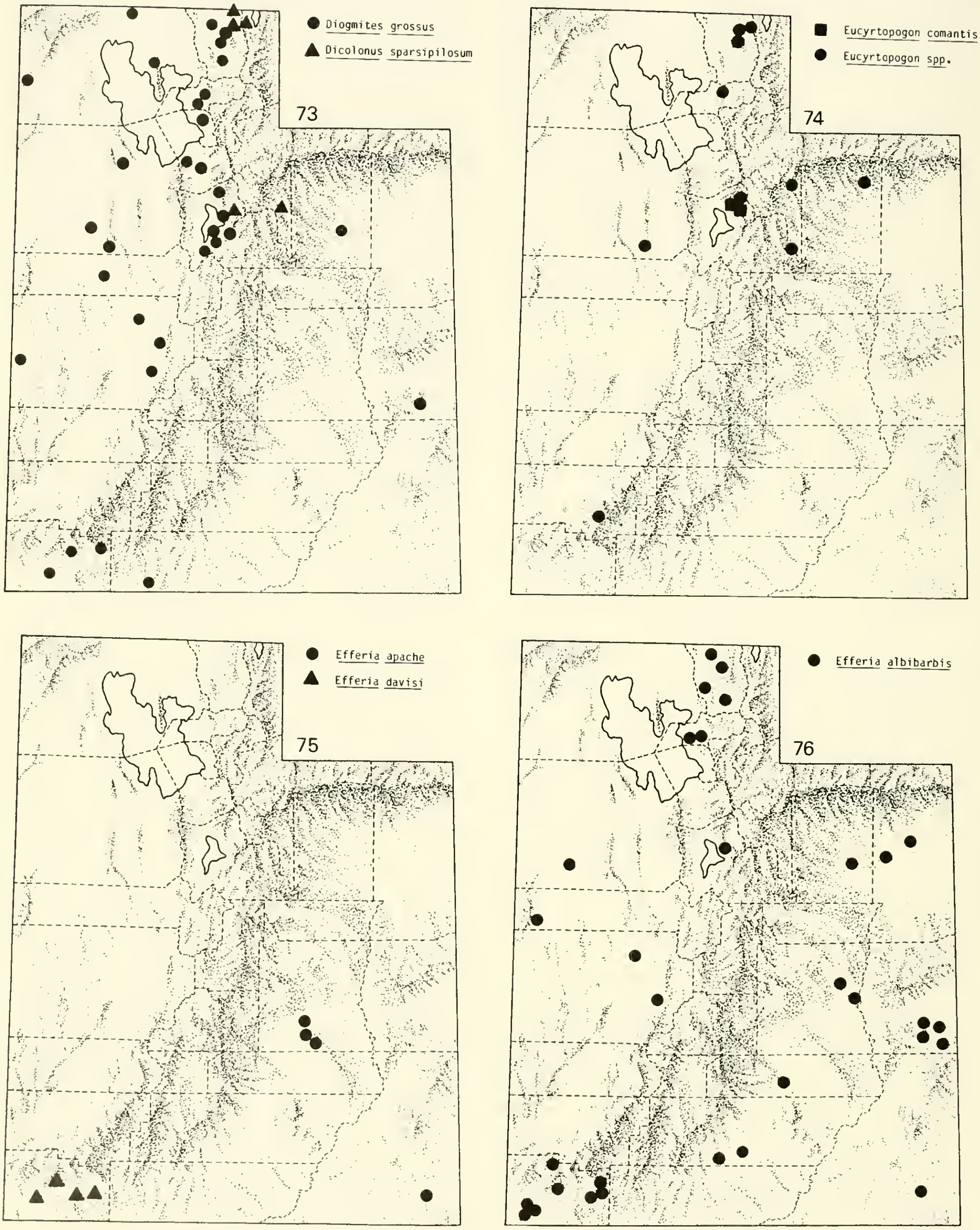
[6] Authors including M. T. James, J. Wilcox, and S. W. Bromley have identified these three species as occurring in Utah. I have difficulty, however, in seeing a distinct brownish tinge of the wings of *P. milberti*, making the male specimens determined by these people run to *P. micans* in Hine's key (1911). Females labelled *P. milberti* lack the spines on the terminal keellike sternites. The dorsal circlet of spines of *P. milberti* is composed of several rows (2–4) of spines, while those of *P. micans* and *P. nearno* are reduced to a single row of stouter spines. These observations were made without examining types but by comparing specimens in the USU collection which had previously been identified by the above authors.


● Diogmites grossus
▲ Dicolonus sparsipilosum
73
■ Eucyrtopogon comantis
● Eucyrtopogon spp.
74
● Efferia apache
▲ Efferia davisi
75
● Efferia albibarbis
76

Figs. 73–76. Utah Asilidae, distribution: 73, *Diogmites grossus* and *Dicolonus sparsipilosum*; 74, *Eucyrtopogon comantis* and *Eucyrtopogon* spp.; 75, *Efferia apache* and *Efferia davisi*; 76, *Efferia albibarbis*.

Daggett Co.: Sheep Creek; Millard Co.: Kanosh; Tooele Co.: Cedar Mountains. 26 March–4 May.

Comantella rotgeri James 1937b: 61 [Holotype: male, Stollsteimer, Colorado, 6,500 ft, 29 October 1935, no repository listed]. Utah distribution: Iron Co.: Cedar City. 26 October.

Cophura albosetosa **Hine** 1908: 202 [Syntypes: two males and one female, Hope Mountains, B.C.; probably in OSU]. Utah distribution: Cache Co.: Green Canyon; Weber Co.: Willard Peak. 21 July–13 August.

Cophura brevicornis **Williston** 1883: 22 [Syntypes: Two specimens, sex not known, from Washington, in KU]. Utah distribution: Uintah Co.: Whiterocks Canyon; Washington Co.: Zion National Park; Wayne Co.: near Grover. 12 July–7 August.

Cophura pollinosa **Curran** 1930: 10 [Holotype: male, Kitt Peak, Rincon, Baboquivari Mountains, Arizona, 1–4 August 1916, 4,050 ft, in AMNH]. Utah distribution: Washington Co.: Santa Clara, Zion National Park. 30 May–27 July.

Cophura scitula **Williston** 1883: 19 [Holotype: sex not known, Washington Territory, in KU]. Utah distribution: Cache Co.: Green Canyon, Logan, Logan Canyon, Tony Grove, West Hodges Canyon; Grand Co.: Wilson Mesa; Rich Co.: Logan Canyon summit; Sanpete Co.: Ephraim Canyon; Utah Co.: American Fork Canyon, Aspen Grove, Emerald Lake. 10 July–23 September.

Cyrtopogon ablautoides **Melander** 1923a: 111 [Syntypes: four males and six females, Mabton, Washington, 3 May 1911, in Melander Collection]. Utah distribution: Millard Co.: 15 mi N Delta. 31 May.

Cyrtopogon albifacies **Johnson** 1942: 1 [Holotype: male, Glacier Lake, Mount Timpanogos, Utah, 10,600 ft; August 1928, in BYU]. Utah distribution: Utah Co.: type locality. July–August.

Cyrtopogon auratus **Cole** in Cole and Lovett, 1919: 230 [Holotype: male, Mt. Rainier, Washington, White River Camp, 4 September 1932, in CAS]. Utah distribution: Cache Co.: Logan, Logan Canyon; Duchesne Co.: Mirror Lake; Rich Co.: Monte Cristo; Summit Co.: Trial Lake. 5 August–14 August.

Cyrtopogon banksi **Wilcox and Martin** 1936: 79 [Holotype: male, Puyallup, Washington; 3 June 1933, in CAS]. Utah distribution: Cache Co.: Avon, Blacksmith Fork Canyon, Cold Spring–Mendon, Providence, Smithfield, Tony Grove, Twin Creek, Wellsville; Daggett Co.: Ashley National Forest, Elk Park; Grand Co.: La Sal Mountains; Juab Co.: Mount Nebo; Rich Co.: Garden City, Logan Canyon summit, Monte Cristo; Utah Co.: American Fork Canyon, Aspen Grove, Mt. Timpanogos, North Fork Provo Canyon; Wasatch Co.: Wolf Creek Pass. 12 June–14 August.

Cyrtopogon bimacula **(Walker)** 1851: 102 [Syntypes: Four males and four females; 'North America,' in British Museum]. Utah distribution: Beaver Co.: Beaver; Duchesne Co.: Wolf Creek Pass; Garfield Co.: Boulder Mountain, Aquarius Plateau; Iron Co.: Cedar Breaks; San Juan Co.: La Sal; Sanpete Co.: Ephraim, Gunnison. 10 July–24 July.

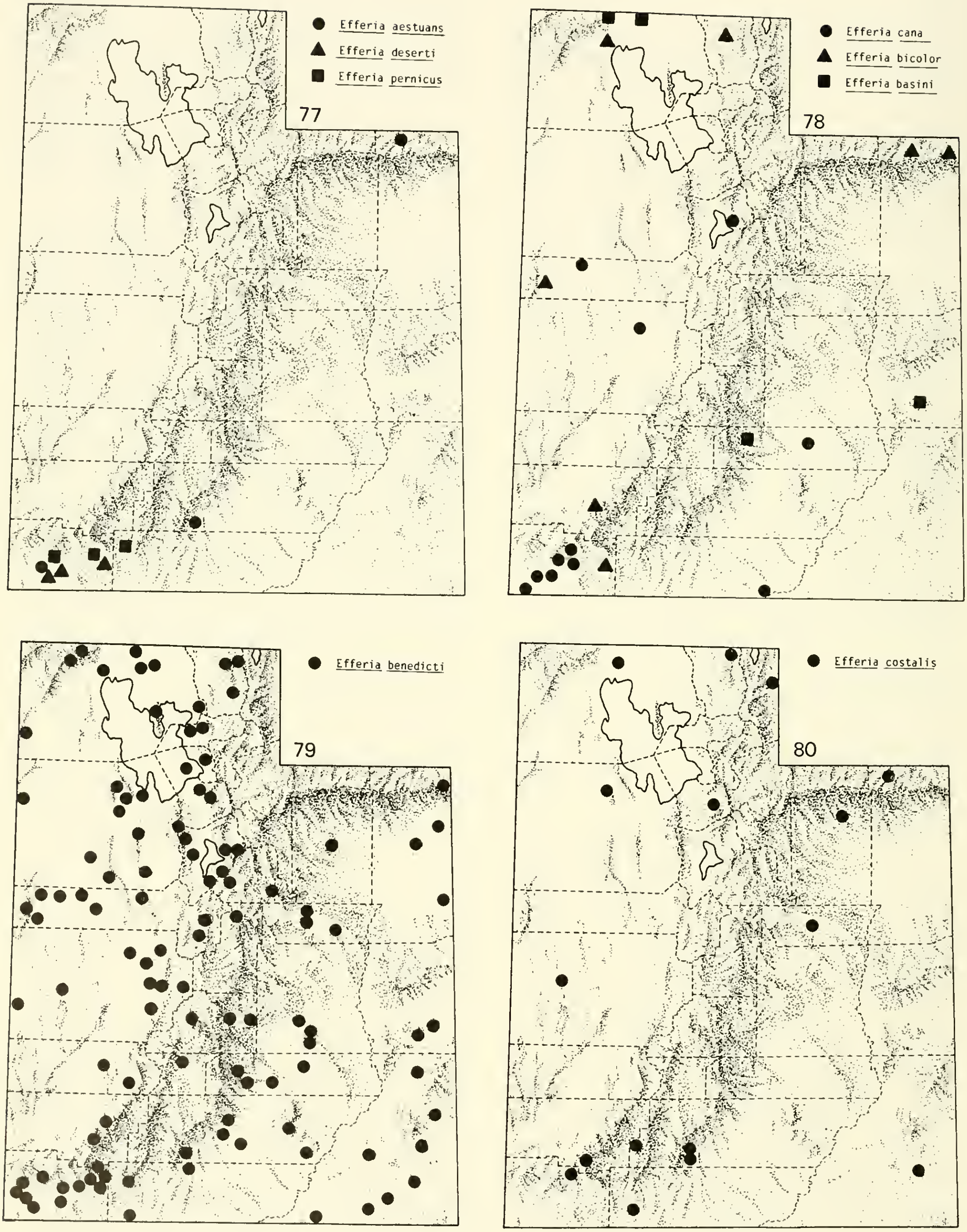
Cyrtopogon curtistylus **Curran** 1923a: 133 [Holotype: male, Cache Junction, Utah, 3 June 1912, in C. W. Johnson collection]. Utah distribution: Box Elder Co.: Brigham City, Willard; Cache Co.: Cache Junction, Beaver Creek, Logan, Logan Canyon, Sardine Canyon; Davis Co.: Bountiful; Rich Co.: Logan Canyon summit; Utah Co.: Glacier Park, Timpanogos, 2 mi W Cascade Springs, Pumphouse Hill. 2 July–3 August.

Cyrtopogon dasylloides **Williston** 1883: 11 [Holotype: male, Washington Territory, in KU]. Utah distribution: Cache Co.: Blacksmith Fork Canyon, Logan. 16 May–12 June.

Cyrtopogon idahoensis **Wilcox and Martin** 1936: 82 [Holotype: male, Parma, Idaho, 13 May 1934, in CAS]. Utah distribution: Cache Co.: Blacksmith Fork Canyon, Cold Spring–Mendon, Logan, Mendon, Sardine Canyon; Garfield Co.: Aquarius Plateau; Rich Co.: Monte Cristo; San Juan Co.: Bear Ears; Utah Co.: Payson Canyon; Weber Co: 13 mi S Monte Cristo. 9 June–23 July.

Cyrtopogon jemezi **Wilcox and Martin** 1936: 47 [Holotype: male, Valle Grande, Jemez Mountains, New Mexico, 6 July 1930, in CAS]. Utah distribution: Grand Co.: Lake Oowah; Uintah Co.: Brownie Canyon. 10 June–22 July.

Cyrtopogon montanus **Loew** 1874: 362 [Holotype: male, Sierra Nevada, in MCZ]. Utah distribution: Box Elder Co.: Willard Peak; Cache Co.: Card Canyon, Dry Canyon, Franklin Basin, Green Canyon, West Hodges Canyon, Hyrum, Logan, Mount Naomi,


● Efferia aestuans
▲ Efferia deserti
■ Efferia pernicus
77
● Efferia cana
▲ Efferia bicolor
■ Efferia basini
78
● Efferia benedicti
79
● Efferia costalis
80

Figs. 77–80. Utah Asilidae, distribution: 77, *Efferia aestuans*, *Efferia deserti*, and *Efferia pernicus*; 78, *Efferia cana*, *Efferia bicolor*, and *Efferia basini*; 79, *Efferia benedicti*; 80, *Efferia costalis*.

Providence, Tony Grove, Wellsville Mountains; Daggett Co.: Summit Springs; Duchesne Co.: Duchesne, Mirror Lake, Wolf Creek Pass, Yellowstone Ranger Station; Garfield Co.: Aquarius Plateau; Juab Co.: Mount Nebo Loop; Rich Co.: Logan Canyon summit; San Juan Co.: Blanding; Sevier Co.: Highway 4; Summit Co.: Bear River Ranger Station, Beaver Creek Ranger Station; Uintah Co.: Brownie Canyon, Brush Creek; Washington Co.: Pine Valley Mountains. 12 May–15 July.

***Cyrtopogon plausor* Osten Sacken** 1877: 297 [Syntypes: four males and two females, no locality listed, in MCZ]. Utah distribution: Cache Co.: Cache Valley; Garfield Co.: Aquarius Plateau, Boulder Mountain; Grand Co.: La Sal Mountains; San Juan Co.: Blanding, Elk Ridge; Summit Co.: Bear River Ranger Station; Utah Co.: Aspen Grove; Wasatch Co.: Strawberry Valley; Washington Co.: Pine Valley, Zion National Park; Wayne Co.: Bicknell, Boulder Mountain, Hanksville; Weber Co.: Farr West. 4 June–10 August.

***Cyrtopogon profusus* Osten Sacken** 1877: 305 [Syntypes: male and female, Morino Valley, New Mexico, 1 July, in MCZ]. Utah distribution: Grand Co.: La Sal Mountains; Utah Co.: Mount Timpanogos. 21 July–17 August.

***Cyrtopogon pulcher* Back** 1909: 274 [Holotype: male, Palmer Lake, Colorado, 10 July, in USNM]. Utah distribution: Box Elder Co.: Devils Gate, Willard Basin; Cache Co.: Beaver Mountain, Blacksmith Fork Canyon, Dry Lake, Logan Canyon, Tony Grove; Daggett Co.: Deep Creek, Sheep Creek; Emery Co.: Green River; Garfield Co.: Boulder Mountain; Rich Co.: Logan Canyon summit; Summit Co.: Bear River Ranger Station; Utah Co.: Aspen Grove, Mount Timpanogos; Wasatch Co.: Daniels Canyon summit; Washington Co.: Leeds. 22 May–14 August.

***Cyrtopogon rufotarsus* Back** 1909: 275 [Holotype: male, Gallatin Co., Montana, 8,000–9,000 ft, 9–11 July, in University of Massachusetts collection]. Utah distribution: Duchesne Co.: Mirror Lake, Uinta Mountains; Grand Co.: Geyser Pass; Kane Co.: Long Valley; Sanpete Co.: Ephraim Canyon; Summit Co.: Trial Lake. 14 June–13 August.

***Cyrtopogon stenofrons* Wilcox and Martin** 1936: 52 [Holotype: male, Grant Co., New Mexico, 24 June 1934, in CAS]. Utah distribution: Cache Co.: Logan; Wayne Co.: Capitol Reef. 1 September–17 October.

***Cyrtopogon thompsoni* Cole** in Cole and Lovett, 1921: 255 [Syntypes: male and female, Burns, Oregon, May 1919, in CAS]. Utah distribution: Box Elder Co.: Curlew Valley; Daggett Co.: Clay Basin; Utah Co.: Goshen Springs. 16 June.

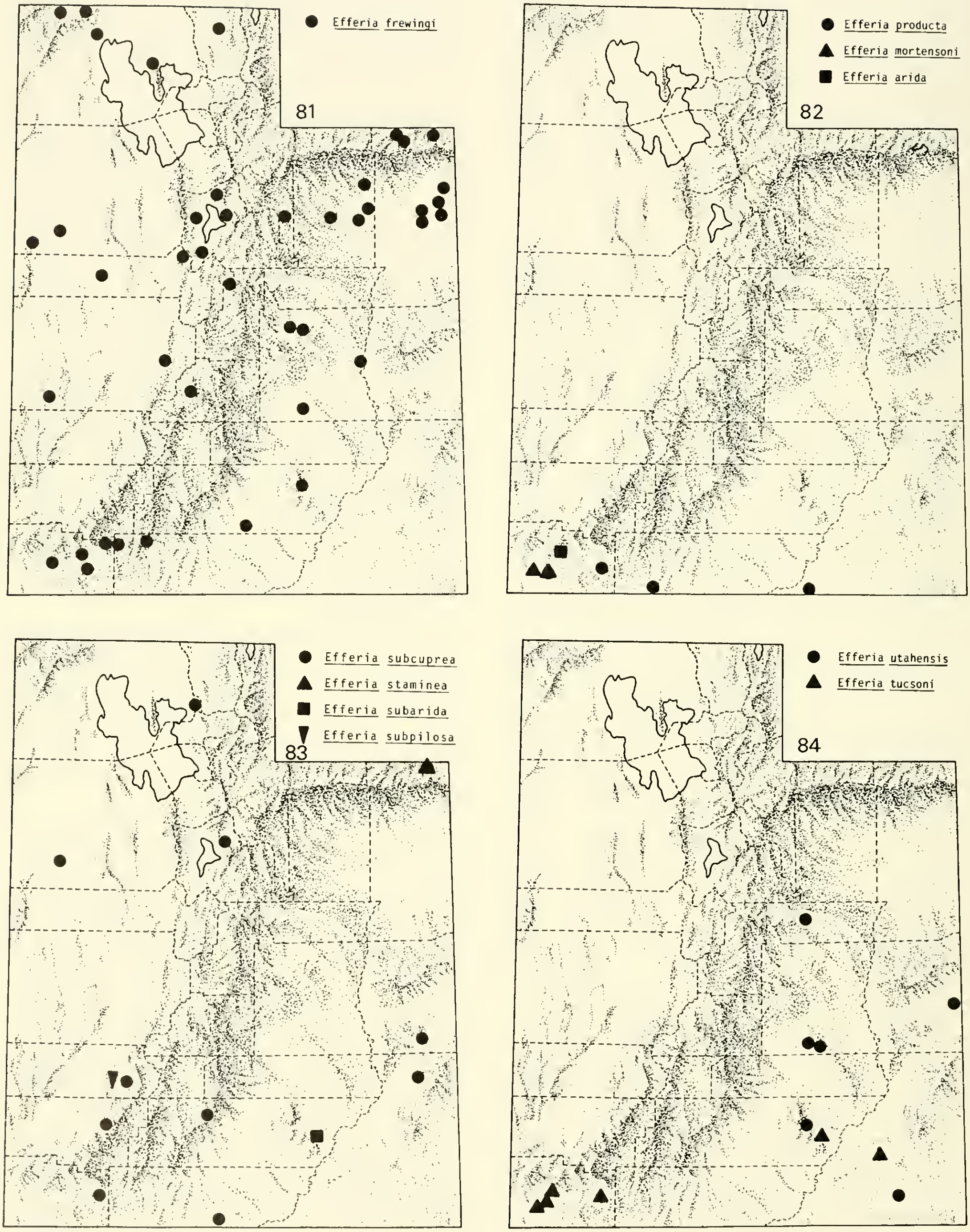
***Cyrtopogon willistoni* Curran** 1922: 277 [Holotype: male, Chilcotin, British Columbia, 16 June 1920, in CNC]. Utah distribution: Box Elder Co.: Devils Gate, Raft River Mtns., Willard Peak; Cache Co.: Franklin Basin, Logan, Logan Canyon, Mount Naomi, Providence, Sardine Canyon, Tony Grove, Wellsville; Carbon Co.: Carbon Airport; Davis Co.: Bountiful; Grand Co.: Geyser Pass, Lake Warner, La Sal Mountains, Miners Basin, Moab; Iron Co.: Parowan Canyon; Juab Co.: Trout Creek; Millard Co.: Kanosh, Oak Creek Canyon; Rich Co.: Bear Lake Valley, Garden City, Logan Canyon summit, Walton (Allen) Canyon; San Juan Co.: La Sal Mtns., Wilson Mesa; Uintah Co.: Whiterocks; Wasatch Co.: Strawberry Valley; Washington Co.: Leeds, Pine Valley, Zion National Park; Weber Co.: Monte Cristo. 16 May–14 August.

***Dicolonus sparsipilosum* Back** 1909: 247 [Cotypes: Two males, Bozeman, Montana, in Univ. of Mass. and Montana State Univ.]. Utah distribution: Cache Co.: Franklin Basin, Tony Grove; Rich Co.: Logan Cyn. summit; Utah Co.: Provo Cyn.; Wasatch Co.: Strawberry Valley. 1–17 July.

***Dioctria henshawi* Johnson** 1918: 103 [Holotype: Yakima, Washington, 2 July 1882, in MCZ #10036]. Utah distribution: Cache Co.: Green Cyn., Spring Hollow; Rich Co.: Logan Cyn. summit, Walton (Allen) Cyn.; Summit Co.: 10 mi E Kamas; Utah Co.: Oquirrh Mtns., Provo; Washington Co.: Pine Valley, St. George; Weber Co.: Ogden. 20 July–5 September.

***Dioctria pusio* Osten Sacken** 1877: 288 [Holotype: Female, Sonoma Co., California, 4 July, in MCZ]. Utah distribution: Utah Co.: Castella. 22 August.

***Dioctria vera* Back** 1909: 256 [Holotype: Male, Monterrey Co., California, 2 July 1896, in AMNH]. Utah distribution: Cache Co.: Logan; Duchesne Co.: Whiterocks; Garfield Co.: Boulder Mtn.; Grand Co.: Castleton; Juab Co.: Deep Creek Mtns. near Callao; Kane Co.: Mt. Carmel; Millard Co.: Kanosh


81
● Efferia frewingi
82
● Efferia producta
▲ Efferia mortensoni
■ Efferia arida
83
● Efferia subcuprea
▲ Efferia staminea
■ Efferia subarida
▼ Efferia subpilosa
84
● Efferia utahensis
▲ Efferia tucsoni

Figs. 81–84. Utah Asilidae, distribution: 81, *Efferia frewingi*; 82, *Efferia producta*, *Efferia mortensoni*, and *Efferia arida*; 83, *Efferia subcuprea*, *Efferia staminea*, *Efferia subarida*, and *Efferia subpilosa*; 84, *Efferia utahensis* and *Efferia tucsoni*.

Cyn., Oak Cr. Cyn.; San Juan Co.: La Sal Mtns., Mill Cr.; Washington Co.: Deep Cr., Leeds, Pine Valley; Wayne Co.: Grover. 13 June–20 August.

Diogmites grossus **Bromley** 1936: 236 [Holotype: Male, Lamar, Prower Co., Colorado, 25 August 1925, in Bromley Collection]. Utah distribution: Box Elder Co.: Pilot Range, Promontory, Snowville; Cache Co.: Cornish, Dry Cyn., Hyrum, Logan, Providence; Davis Co.: Clearfield; Duchesne Co.: Bluebell; Grand Co.: Moab; Juab Co.: Topaz Mtn.; Kane Co.: Kanab; Millard Co.: Delta, Flowell, Garrison, Holden; Salt Lake Co.: Magna, Midvale; Tooele Co.: Camelback, Little Granite Mtn., Skull Valley, Simpson Butte; Utah Co.: Alpine, Goshen, Hobble Cr., Lincoln Beach, Provo, Rock Cyn., Spanish Fork; Washington Co.: Leeds, St. George, Zion National Park; Weber Co.: Ogden, South Weber. 30 July–11 September.

Eucyrtopogon comantis **Curran** 1923a: 116 [Holotype: Male, Chilcotin, B.C., 29 April 1920, in CNC #565]. Utah distribution: Utah Co.: Aspen Grove, Emerald Lake, Glacier Lake, Mount Timpanogos. No dates with labels.

Eucyrtopogon **spp.** Utah distribution: Cache Co.: Dry Cyn., Logan Cyn., Logan Peak, Twin Cr.; Duchesne Co.: Forest Camp, Uintah Cyn., Uinta Mtns., Wolf Cr.; Iron Co.: Cedar City; Rich Co.: Logan Cyn. summit; Tooele Co.: Vernon Cr.; Utah Co.: Aspen Grove; Wasatch Co.: Soldier Summit; Weber Co.: Eden.

Haplopogon utahensis **Wilcox** 1966d: 99–106 [Holotype: Male, 7 mi N St. George, Utah, Hwy 91, 1 June 1963, in CAS]. Utah distribution: Washington Co.: Washington. 1–8 June.

Heteropogon arizonensis **Wilcox** 1941: 55 [Holotype: Male, White Mtns., Arizona, September, in CAS]. Utah distribution: Millard Co.: Oak City. 6–25 June.

Heteropogon maculinervis **James** 1937a: 12 [Holotype: Female, Masonville, Colorado, 4 Sep 1934, in CSU]. Utah distribution: Beaver Co.: 9 mi E Beaver; Box Elder Co.: Clear Cr., Fielding; Cache Co.: Avon Cyn., Green Cyn., Providence, Twin Cr.; Daggett Co.: Pipe Cr.; Grand Co.: La Sal Mtns.; Iron Co.: Cedar City; Kane Co.: Zion—Chamberlain Ranch; Tooele Co.: Granite Mtn., Johnsons Pass; Uintah Co.: Little Mtn., Summit, Utah State Exp. Sta.; Utah Co.: Payson Cyn., West Cyn.; Wasatch Co.: Soldier Summit; Washington Co.: Zion National Park; Weber Co.: Huntsville. 6 August–4 September.

Heteropogon martini **Wilcox** 1965: 207 [Holotype: Male, Montgomery Pass, Nevada, 6 July 1958, in Wilcox Collection in CAS]. Utah distribution: Box Elder Co.: Snowville; Cache Co.: Logan, Wellsville Cyn.; Daggett Co.: Sheep Cr.; Davis Co.: Clearfield; Emery Co.: 4 air mi N Gilson Butte; Millard Co.: Fillmore, warm spring near Gandi; Utah Co.: Fairfield, west side Utah Lake, Lehi. 16 June–4 September.

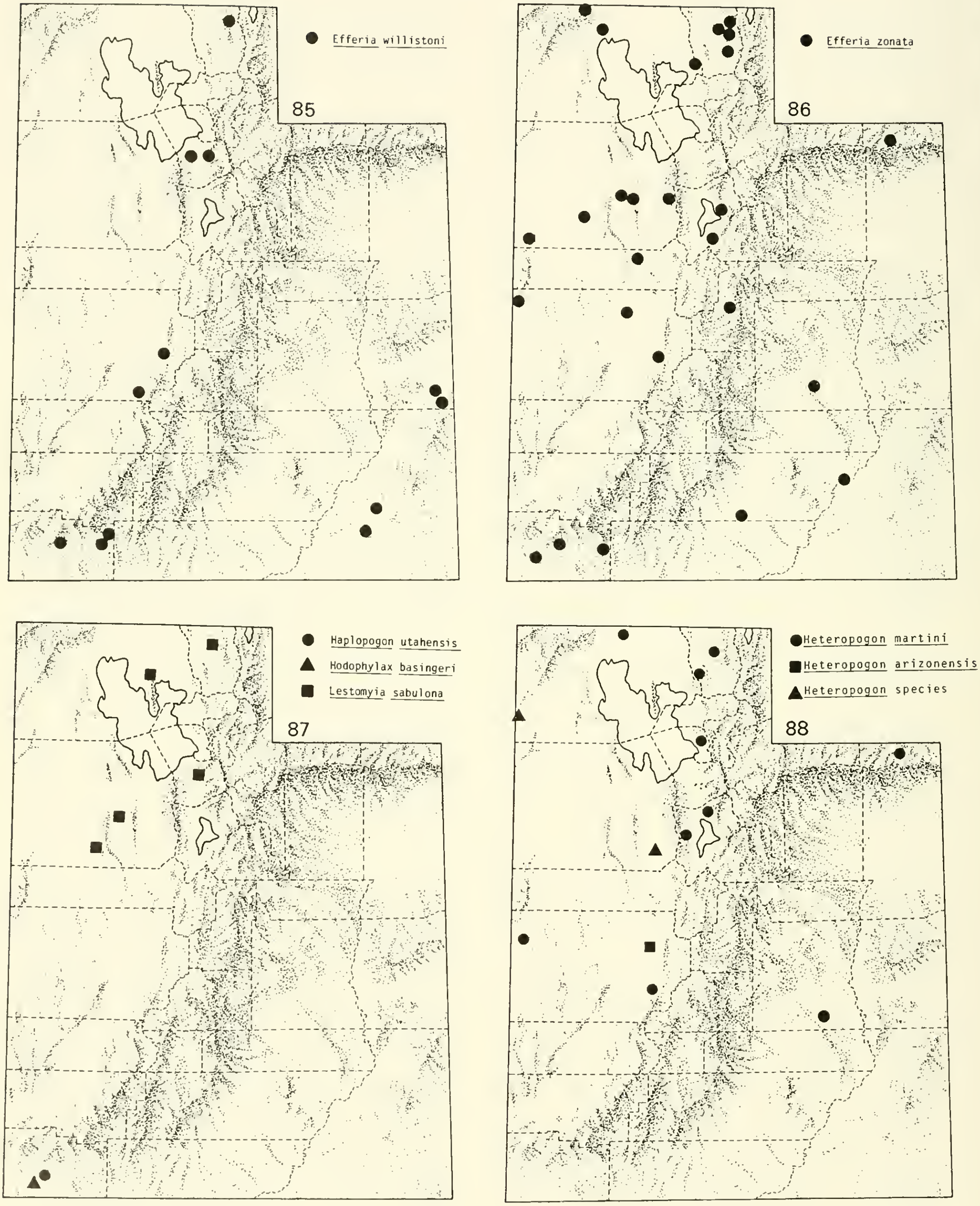
Heteropogon senilis **(Bigot)** 1878: 423 [Holotype: sex not known, California, in Bigot collection]. Utah distribution: Box Elder Co.: Lucin, 1 mi NE Mantua; Cache Co.: Card Cyn., Green Cyn., Logan Cyn.; Daggett Co.: Palisade Park Camp; Iron Co.: Kanarraville, near Parowan; Millard Co.: Oak Cr. Cyn.; Utah Co.: American Fork. 16 June–4 September.

Heteropogon stonei **Wilcox** 1965: 207–222 [Holotype: Male, Hualapai Mtns., Arizona, 6,000 ft, 4 June 1962, in CAS]. Utah distribution: Beaver Co.: Beaver Cyn. No date given.

Heteropogon **species 1.** Two specimens, undescribed. Utah distribution: Box Elder Co.: Tecoma Range—Copper Mtns.; Tooele Co.: Lofgreen. No dates on labels.

Hodophylax basingeri **Pritchard** 1938: 130 [Holotype: Female, Quail Spring, San Bernardino Co., California, 5 October 1934, in Basinger collection]. Utah distribution: Washington Co.: St. George. No date on label.

Holopogon albipilosus **Curran** 1923b: 207 [Holotype: Male, Vernon, B.C., 5 August 1920, in CNC #569]. Utah distribution: Beaver Co.: Beaver, Greenville, 9 mi E Beaver; Box Elder Co.: Park Valley, Portage; Cache Co.: Ant Valley, Blacksmith Fork Cyn., Logan, Mendon; Duchesne Co.: Duchesne, Fort Duchesne, Tabiona, Whiterocks; Garfield Co.: Panguitch; Grand Co.: Dead Horse Point, Green River, 378 river mile; Iron Co.: Paragonah, Parowan; Juab Co.: Nephi, Trout Cr.; Kane Co.: Kanab; Millard Co.: Oak City, Pahvant, Scipio; Morgan Co.: Devils Slide; Piute Co.: Circleville; Rich Co.: Laketown, North Eden, Walton (Allen) Cyn.; Salt Lake Co.: Bluffdale, Magna, Salt Lake City; Sanpete Co.: Indianola, Manti, Moroni;


● Efferia willistoni
85
● Efferia zonata
86
● Haplopogon utahensis
▲ Hodophylax basingeri
■ Lestomyia sabulona
87
● Heteropogon martini
■ Heteropogon arizonensis
▲ Heteropogon species
88

Figs. 85–88. Utah Asilidae, distribution: 85, *Efferia willistoni*; 86. *Efferia zonata*; 87, *Haplopogon utahensis*, *Hodophylax basingeri*, and *Lestomyia sabulona*; 88, *Heteropogon martini*, *Heteropogon arizonensis*, and *Heteropogon* species 1.

Sevier Co.: Elsinore, Glenwood, Richfield; Summit Co.: Red Rock Cyn.; Tooele Co.: Camelback, Dugway Proving Grounds, Little Granite Mtns.; Uintah Co.: Hayden, La Point, Naples, Tridell, Vernal, Whiterocks; Utah Co.: Alpine Loop, Aspen Grove, Lehi, Lindon, North Fork Provo Cyn., Payson, Provo, Provo Cyn., Spring Lake, Springville; Wasatch Co.: Heber, Strawberry Valley; Washington Co.: Pine Valley; Wayne Co.: Cainville, Grover. 1 June–5 August.

Holopogon caesariatus **Martin** 1959: 1–40 [Holotype: Male, Alpha, Long Valley, Idaho, 6 July 1934, in AMNH]. Utah distribution: Cache Co.: Blacksmith Fork Cyn. 7 August.

Holopogon currani **Martin** 1959: 17 [Holotype: Male, Winona, Arizona, 21 July 1949, in AMNH]. Utah distribution: Daggett Co.: Manila; Washington Co.: Leeds Cyn., Zion National Park; Wayne Co.: Grover. 11–28 July.

Holopogon mingusae **Martin** 1959: 21 [Holotype: Male, Mingus Mtn., Arizona, 3 July 1949, in AMNH]. Utah distribution: Garfield Co.: Aquarius Plateau, The Pass; Washington Co.: Zion National Park; Wayne Co.: Grover. 11 July–21 August.

Holopogon wilcoxi **Martin** 1959: 33 [Holotype: Male, San Carlos Lake, Arizona, May, in CAS]. Utah distribution: Beaver Co.: Beaver; Tooele Co.: South Camel Mtn. 13 July.

Laphystia annulata **Hull** 1957: 72 [Holotype: Male, near Navajo, Arizona, 11 July 1954, in Hull collection]. Utah distribution: Kane Co.: Coral Pink Sand Dunes, Mount Carmel Jct. 14 July.

Laphystia rubra **Hull** 1957: 74 [Holotype: Female, near Navajo, Arizona, 11 July 1954, in Hull collection]. Utah distribution: Emery Co.: Goblin Valley, 4 air mi N Gilson Butte, Wild Horse Creek; Grand Co.: Green River, 366 river mile; San Juan Co.: Bluff, Lime Cr. 7 July–26 August.

Laphystia tolandi **Wilcox** 1960: 344 [Holotype: Male, Lahontan Reservoir, Churchill Co., Nevada, 13 June 1949, in CAS]. Utah distribution: Box Elder Co.: Corinne, Locomotive Springs, Tremonton; Cache Co.: Cornish; Juab Co.: Fish Springs, Topaz Mtn.; Millard Co.: Delta, Fillmore; Sevier Co.: Richfield; Tooele Co.: Camelback, Granite Mtn.; Utah Co.: Spanish Fork. 14 June–14 August.

Laphystia utahensis **Wilcox** 1960: 345 [Holotype: Male, St. George, Utah, 12 mi NE Hwy 17, 23 May 1959, in CAS]. Utah distribution: Washington Co.: 12 mi NE St. George (near Hurricane). 22–23 May.

Lasiopogon albidus **Cole and Wilcox** 1938: 25 [Holotype: Male, 8 mi E Kiona, Washington, 23 April 1933, in CAS]. Utah distribution: Emery Co.: Green River (Gunnison Butte); Grand Co.: Moab. 7 May.

Lasiopogon aldrichii **Melander** 1923b: 139 [Syntypes: Male and female, Moscow Mtn., Idaho, 29 June 1918, repository not listed]. Utah distribution: Cache Co.: Logan Cyn.; Duchesne Co.: Roosevelt; Grand Co.: La Sal Mtns.; Rich Co.: Monte Cristo; Uintah Co.: Brush Cr., Whiterocks; Utah Co.: Mt. Timpanogos; Washington Co.: Leeds, Pinto. 24 June–21 July.

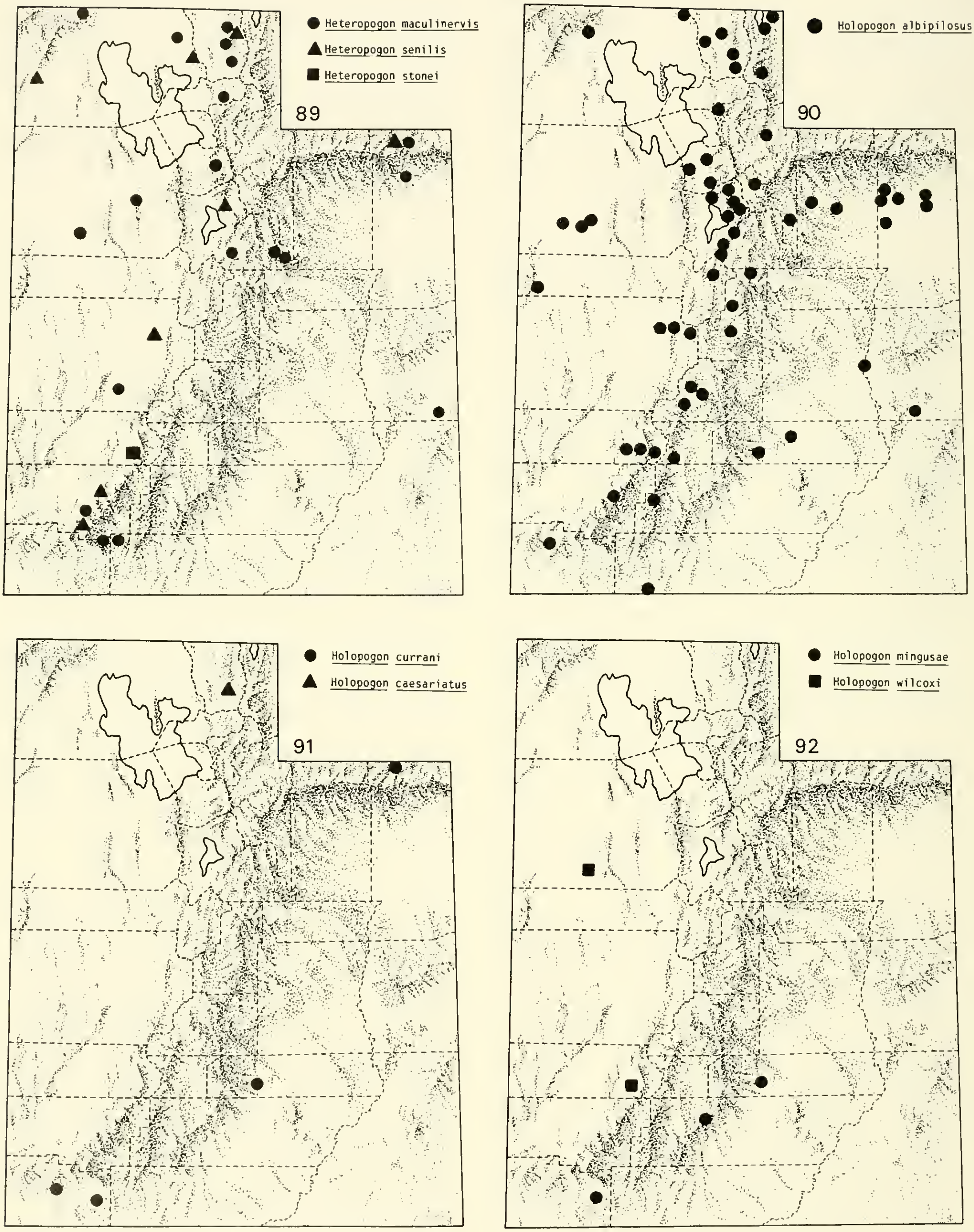
Lasiopogon cinereus **Cole,** ***in*** Cole and Lovett 1919: 229 [Holotype: Male, Hood River, Oregon, 24 September 1918, in CAS #476]. Utah distribution: Daggett Co.: Manila; Duchesne Co.; Uintah Co.: Merkeley Park (near Vernal), Whiterocks; Utah Co.: Hobble Cr. 6 July–16 August.

Lasiopogon monticola **Melander** 1923b: 142 [Syntypes: Males and females, Mt. Adams, Washington, 24 July 1921, no repository listed]. Utah distribution: Cache Co.: Green Cyn., Logan Cyn., Mt. Logan; Grand Co.: Moab, Wilson Mesa–La Sal Mtns.; Rich Co.: Logan Cyn. summit, Monte Cristo; Uintah Co.: Whiterocks; Weber Co.: Ogden. 26 May–9 July.

Lestomyia sabulona **Osten Sacken** 1877: 292 [Syntypes: Male and female, Crafton, near San Bernardino, California, March, on dry gravelly soil, in MCZ]. Utah distribution: Box Elder Co.: Promontory Point; Cache Co.: Logan; Juab Co.: Topaz Mtn.; Salt Lake Co.: Salt Lake City; Tooele Co.: Dugway Proving Grounds, Skull Valley. 24 May–9 June.

Metapogon carinatus **Wilcox** 1964: 193 [Holotype: Male, Whitewater, California, 13 January 1948, in CAS]. Utah distribution: Uintah Co.: Split Mtn. Gorge. Date uncertain, "55-28" (2-8-1955?).

Myelaphus lobicornis **Osten Sacken** 1877: 287 [Holotype: Male, Snake River, Idaho, in MCZ]. Utah distribution: Cache Co.: Blacksmith Fork Cyn., Green Cyn., Hyrum Dam, Logan. 17–22 June.


● Heteropogon maculinervis
▲ Heteropogon senilis
■ Heteropogon stonei
89
● Holopogon albipilosus
90
● Holopogon currani
▲ Holopogon caesariatus
91
● Holopogon mingusae
■ Holopogon wilcoxi
92

Figs. 89–92. Utah Asilidae, distribution: 89, *Heteropogon maculinervis*, *Heteropogon senilis*, and *Heteropogon stonei*; 90, *Holopogon albipilosus*; 91, *Holopogon currani* and *Holopogon caesariatus*; 92, *Holopogon mingusae* and *Holopogon wilcoxi*.

Nannocyrtopogon aristatus **James** 1942: 126 [Holotype: Male, Arboles, Colorado, 6,700 ft, 17 May 1939, in CSU]. Utah distribution: Iron Co.: 5 mi E New Harmony; Washington Co.: Leeds Cyn., Oak Grove. 23 May–6 June.

Nicocles abdominalis **Williston** 1883: 17 [Holotype: Male, California, in KU]. Utah distribution: Washington Co.: Zion National Park. No date on label.

Nicocles utahensis **Banks** 1920: 66 [Holotype: Female, Eureka, Utah, 31 May, in MCZ]. Utah distribution: Cache Co.: Green Cyn., Hyrum, Logan, Logan Cyn., Sardine Cyn., USU; Emery Co.: Green River; Grand Co.: Moab; Juab Co.: Eureka; Salt Lake Co.: Little Mtn.; Utah Co.: Provo. 5 March–5 June.

Omninablautus nigronotum **(Wilcox)** 1935: 1 [Holotype: Male, Prairie Hill, Grant Co., Oregon, in CAS]. Utah distribution: Box Elder Co.: Etna. 12 August.

Ospriocerus abdominalis **(Say)** 1824: 375 [Holotype: Lost]. Utah distribution: Beaver Co.: Minersville; Box Elder Co.: Blue Cr., Collinston, Mantua, Promontory, Snowville; Cache Co.: Beaver Mtn., Cornish, Clarkston, Hyrum, Lewiston, Logan, Mendon, Providence, Smithfield; Daggett Co.: Douglas Dinosaur Quarry, Flaming Gorge; Davis Co.: Farmington; Duchesne Co.: Monarch, Mountain Home, Myton; Emery Co.: 2 mi E Gilson Butte, 9 air mi E Castledale, Sinbad Country, Wild Horse Cr. north of Goblin Valley, Woodside; Grand Co.: Castleton, Moab; Iron Co.: Cedar City; Juab Co.: Deep Cr. Mtns., Fish Springs, Jericho, Levan, Nephi, Trout Cr.; Kane Co.: Kanab; Millard Co.: Delta, Fillmore, Holden, Oasis, Pahvant, Scipio; Rich Co.: Bear Lake Valley, Dry Basin; Sevier Co.: Fremont Jct., Monroe Cyn., Richfield; Tooele Co.: Cedar Mtns., Dugway Proving Grounds, James Ranch, Lakeside Mtns., Little Granite Mtn., Ophir; Uintah Co.: Fort Duchesne, Gusher, 3 mi SW Jensen, Vernal; Utah Co.: Cedar Valley, Lehi, Provo, West Utah Lake; Wasatch Co.: Deer Cr. Reservoir; Washington Co.: Pine Valley, St. George, Zion National Park; Wayne Co.: Notom; Weber Co.: Ogden. 9 June–6 September.

Ospriocerus longulus **(Loew)** 1866: 28 [Holotype: in MCZ]. Utah distribution: Grand Co.: Castleton; Washington Co.: Santa Clara. 8–29 July.

Ospriocerus minos **Osten Sacken** 1877: 291 [Holotype: Male, Golden City, Colorado, 3 July, in MCZ]. Utah distribution: Emery Co.: 3 mi SSE Temple Mtn., San Rafael Desert; Grand Co.: Arches National Monument; Tooele Co.: Dugway Proving Grounds; Uintah Co.: 3 mi SW Jensen, Vernal; Utah Co.: 1 mi W Elberta; Wayne Co.: Notom. 25 July–31 July.

Ospriocerus vallensis **Martin** 1968: 401 [Holotype: Male, Grand View, Owyhee Co., Idaho, 9 July 1958, in CAS]. Utah distribution: Box Elder Co.: Cedar Hills, Steamboat Springs, Thiokol; Cache Co.: Providence; Rich Co.: Sage Cr. Jct.; Sevier Co.: Richfield. 4 June–11 July.

Saropogon mohawki **Wilcox** 1966b: 134 [Holotype: Male, Mohawk, Arizona, 16 July 1962, in CAS]. Utah distribution: Washington Co.: Ivins. 16 July.

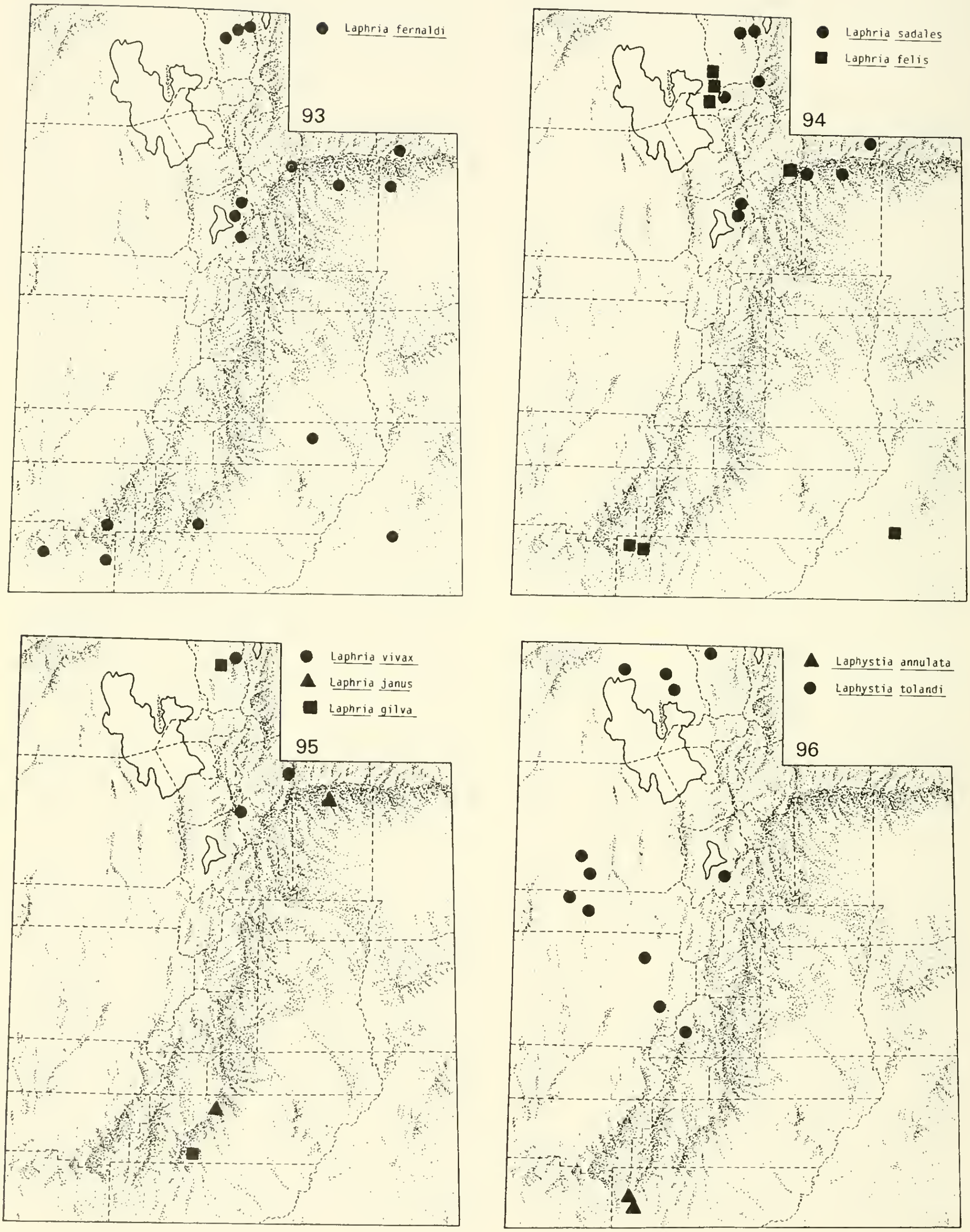
Scleropogon bradleyi **(Bromley)** 1937a: 309 [Holotype: Male (female on same pin), Grant Forest, California, 9–13 August 1937, in USNM]. Utah distribution: Wayne Co.: 6 mi W Torrey. 15–20 July.

Scleropogon coyote **(Bromley)** 1931: 429 [Syntypes: Male and female, near Lander, Wyoming, July, in OSU]. Utah distribution: Emery Co.: 4 air mi N Gilson Butte; Grand Co.: La Sal Mtns.; Utah Co.: Colton. 20–23 July.

Scleropogon duncani **(Bromley)** 1937a: 307 [Holotype: Male, Silver City, New Mexico, 24 June 1933, in CAS]. Utah distribution: Washington Co.: Rockville, Santa Clara, Zion National Park. 22–24 June.

Scleropogon indistinctus **(Bromley)** 1937a: 308 [Syntypes: Male and female, White Mtns., Arizona, August 1930, in CAS]. Utah distribution: Cache Co.: Logan Cyn., Providence; Daggett Co.: Hideout Cyn., Pipe Cr.; Juab Co.: Nephi; Millard Co.: Antelope Springs; Salt Lake Co.: Salt Lake City; Sevier Co.: Richfield. 26 May–16 August.

Scleropogon neglectus **(Bromley)** 1931: 430 [Syntypes: Male and Female, near Lander, Wyoming, August, in OSU]. Utah distribution: Beaver Co.: Beaver; Box Elder Co.: Clear Cr., Yost; Cache Co.: Beaver Mtn., Hyrum, Logan, Providence; Daggett Co.: Hideout Cyn., Manila; Emery Co.: Buckskin Springs, Goblin Valley; Garfield Co.: Boulder Mtn., 15 mi N Boulder; Grand Co.: La Sal Mtns.; Juab Co.: Callao, Topaz Mtn.; Millard


Laphria fernaldi
93
Laphria sadales
Laphria felis
94
Laphria vivax
Laphria janus
Laphria gilva
95
Laphystia annulata
Laphystia tolandi
96

Figs. 93–96. Utah Asilidae, distribution: 93, *Laphria fernaldi*; 94, *Laphria sadales* and *Laphria felis*; 95, *Laphria vivax*, *Laphria janus*, and *Laphria gilva*; 96, *Laphystia annulata* and *Laphystia tolandi*.

Co.: Fillmore, Sutherland; Piute Co.: Utah Agricultural Research Station; Rich Co.: Woodruff; Tooele Co.: Camelback, Dugway Proving Grounds, Lakeside Mtns.; Washington Co.: Toquerville. 29 May–16 August.

Scleropogon picticornis **Loew** 1866: 26 [Holotype: Female, California, in MCZ]. Utah distribution: Kane Co.: Kanab; San Juan Co.: Bluff. 20 August–12 September.

Sintoria cazieri **Wilcox** 1972a: 51 [Holotype: Male, Holden, Utah, 18 September 1959, in AMNH]. Utah distribution: Emery Co.: Goblin Valley; Iron Co.: Beryl; Millard Co.: Holden; Washington Co.: Beaver Dam Slope on Joshua Trees, Red Cliffs Cmpgd. at lights; Weber Co.: Five Points. 16–27 September.

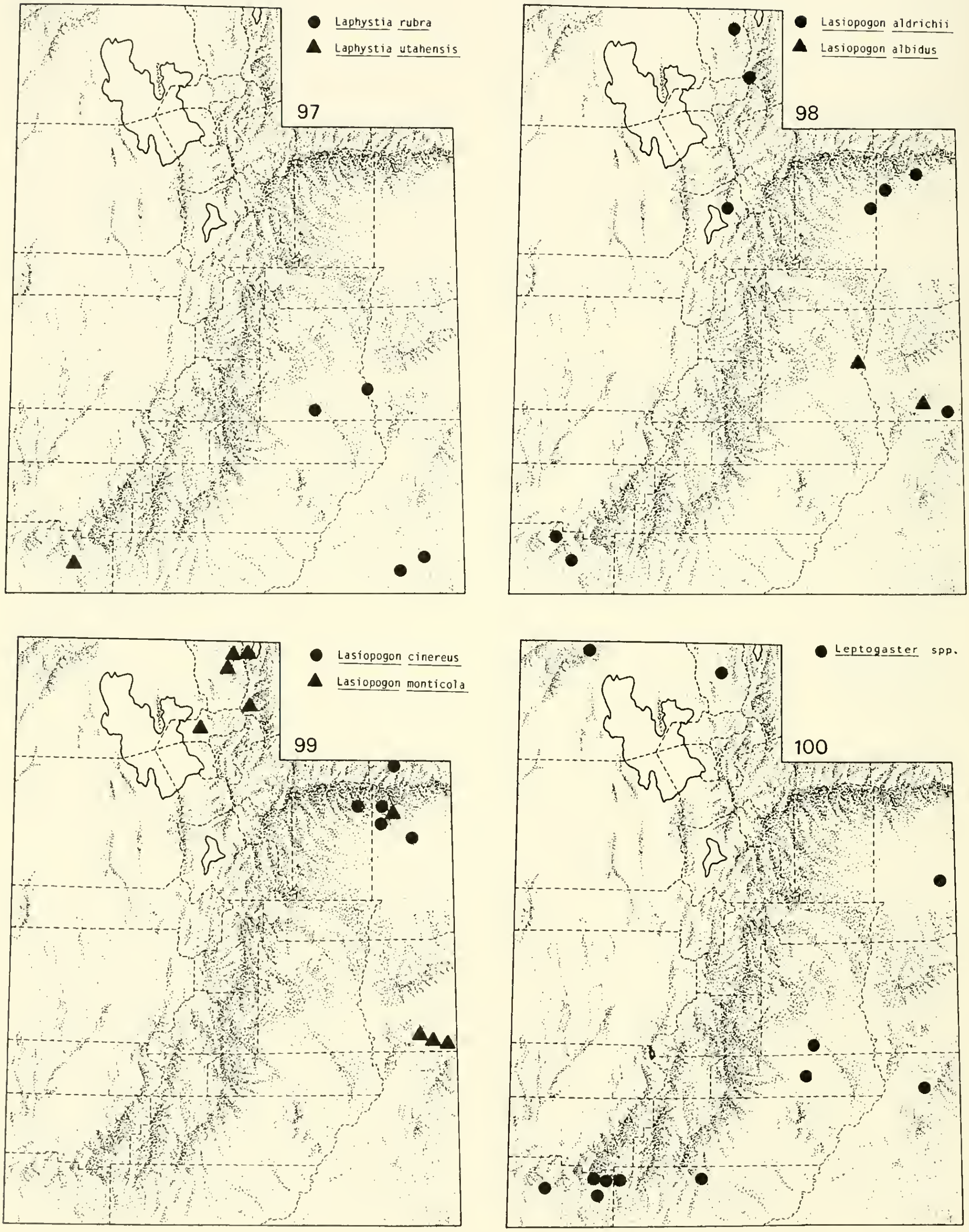
Stenopogon engelhardti **Bromley** 1937a: 301 [Syntypes: Male and female, Jacumba, California, 26 April 1935, in CAS]. Utah distribution: Box Elder Co.: Raft River Mtns.; Cache Co.: Blacksmith Fork Cyn., Logan Cyn., Tony Grove, Wellsville Cyn.; Daggett Co.: Elk Park; Duchesne Co.: 30 mi SW Duchesne; Garfield Co.: Boulder Mtn., Bryce Cyn.; Iron Co.: Cedar City; Juab Co.: Eureka; Rich Co.: Logan Cyn. summit; Salt Lake Co.: Dry Cyn., Little Mtn., Salt Lake City; Sanpete Co.: Indianola; Sevier Co.: Richfield; Tooele Co.: Lookout Mtn., Stansbury Island; Utah Co.: Alpine, Aspen Grove, Payson Cyn., Provo; Washington Co.: Zion National Park; Wayne Co.: Hanksville. 8 June–14 August.

Stenopogon inquinatus **Loew** 1866: 27 [Syntypes: Male and female, Nebraska, in MCZ]. Utah distribution: Beaver Co.: Milford; Box Elder Co.: Cedar Cr., Clear Cr., Cutler Dam, Devils Gate, Mantua, Washakie; Cache Co.: Green Cyn., Logan, Logan Cyn., Providence, Tony Grove, Wellsville Cyn.; Carbon Co.: Dragerton, Price, Woodhill; Daggett Co.: Flaming Gorge, Hideout Cyn., Manila, Spirit Lake Road, Summit Ranger Station; Duchesne Co.: Roosevelt, Yellowstone Ranger Station; Garfield Co.: Boulder Mtn., Bryce Cyn., Escalante, Panguitch Lake, Tropic; Grand Co.: La Sal Mtns., Westwater; Iron Co.: Parowan Cyn.; Juab Co.: Fish Springs, Trout Cr.; Millard Co.: Fillmore, Oak Cr. Cyn.; Piute Co.: Marysvale; Rich Co.: Bear Lake Valley, Laketown, Logan Cyn. summit, Woodruff; Salt Lake Co.: Big Cottonwood Cyn., Parleys Cyn., Salt Lake City; San Juan Co.: Bear Ears; Sanpete Co.: Gunnison, Indianola; Sevier Co.: Gooseberry, USDA (center of county); Tooele Co.: Dugway Proving Grounds, Timpie; Uintah Co.: Douglas, Fort Duchesne, Vernal; Utah Co.: Aspen Grove, Provo Cyn.; Washington Co.: Dixie Park (Snow Cyn.), Zion National Park; Wayne Co.: Boulder Mtn., Hanksville. 8 May–29 July.

Stenopogon martini **Bromley** 1937a: 303 [Syntypes: Male and female, Parma, Idaho, 13 May 1934, in CAS]. Utah distribution: Box Elder Co.: Collinston, Fielding, Snowville; Cache Co.: Blacksmith Fork Cyn., Cornish, Logan; Daggett Co.: Manila; Davis Co.: Antelope Island, Bountiful, Farmington; Duchesne Co.: Bluebell, Roosevelt; Garfield Co.: Panguitch, Panguitch Lake; Grand Co.: Moab; Iron Co.: Miners Peak, Parowan Cyn.; Juab Co.: Eureka, Topaz Mtn.; Millard Co.: Delta, Hatton, McCormick; Rich Co.: Garden City, Laketown, Walton (Allen) Cyn.; Salt Lake Co.: Taylorsville; Sanpete Co.: Fountain Green, Indianola, Seely Cr.; Summit Co.: Elk Park Cmpgd.; Tooele Co.: Grantsville, Stansbury Island, Timpie, Vernon Cyn.; Uintah Co.: Fort Duchesne, Vernal; Utah Co.: Aspen Grove, Provo, Spanish Fork; Wasatch Co.: Strawberry Valley; Wayne Co.: Fremont, Torrey; Weber Co.: Ogden, Ogden Cyn., Riverdale. 15 May–6 September.

Stenopogon mexicanus **Cole** 1923: 463 [Holotype: Male, Guaymas, Sonora, Mexico, 10 April 1921, in CAS #1341]. Utah distribution: Cache Co.: Logan; Grand Co.: Castleton. 24 July–1 September.

Stenopogon rufibarbis **Bromley** 1931: 431 [Holotype: Male, Lassen Co., California, 20 July 1911, in OSU]. Utah distribution: Beaver Co.: Beaver Cr.; Box Elder Co.: Devils Gate, Raft River Mtns., Willard Peak; Cache Co.: Blacksmith Fork Cyn., Card Cyn., Logan, Newton, Sardine Cyn., Wellsville; Daggett Co.: Manila; Duchesne Co.: Duchesne; Garfield Co.: Aquarius Plateau, The Pass; Grand Co.: Castle Valley, Moab (La Sal Mtns.); Iron Co.: Cedar City; Juab Co.: Eureka, Mt. Nebo; Kane Co.: Alton, Long Valley; Rich Co.: Garden City; Salt Lake Co.: Salt Lake City; San Juan Co.: Geyser Pass; Sanpete Co.: Fountain Green; Summit Co.: Park City; Tooele Co.: Tooele; Uintah Co.: Vernal; Utah Co.: Alpine, Aspen Grove, Spanish


● Laphystia rubra
▲ Laphystia utahensis
97
● Lasiopogon aldrichii
▲ Lasiopogon albidus
98
● Lasiopogon cinereus
▲ Lasiopogon monticola
99
● Leptogaster spp.
100

Figs. 97–100. Utah Asilidae, distribution: 97, *Laphystia rubra* and *Laphystia utahensis*; 98, *Lasiopogon aldrichii* and *Lasiopogon albidus*; 99, *Lasiopogon cinereus* and *Lasiopogon monticola*; 100, *Leptogaster* spp.

Fork; Washington Co.: Leeds Cyn., Pine Valley; Wayne Co.: Hanksville; Weber Co.: Ogden. 20 May–25 July.

Stenopogon utahensis **Bromley** 1951: 8 [Syntypes: Male and female, Leeds, Utah, 20 June 1929, in USNM]. Utah distribution: Washington Co.: Leeds, St. George. 1–20 June.

Stichopogon fragilis **Back** 1909: 334 [Holotype: Female, Alamagordo, New Mexico, 24 April 1902, in AESP]. Utah distribution: Emery Co.: San Rafael Desert 3 mi SSE Temple Mtn., 5,300 ft; Millard Co.: Delta; Tooele Co.: Dugway Proving Grounds; Washington Co.: Santa Clara; 3 mi NW St. George. 24 May–4 July.

Stichopogon salinus **(Melander)** 1923c: 216 [Holotype: Male, Great Salt Lake, Utah, 31 July 1908, in Aldrich Collection]. Utah distribution: Beaver Co.: Minersville; Cache Co.: Cornish, Logan; Juab Co.: Topaz Mtn.; Millard Co.: Delta, Hatton, Pahvant; Salt Lake Co.: Great Salt Lake; Utah Co.: Aspen Grove, Goshen, Provo, Spanish Fork, west Utah Lake. 20 June–3 August.

Stichopogon trifasciatus (Say) 1823: 51 [Holotype: Lost]. Utah distribution: Duchesne Co.: Indian Creek, Roosevelt; Kane Co.: Kanab, Zion National Park near east entrance; Uintah Co.: Naples; Washington Co.: Santa Clara, Zion National Park. 25 June–19 August.

Taracticus ruficaudus **Curran** 1930: 4 [Holotype: Female, Mud Springs, Santa Catalina Mtns., Arizona, 17–20 July 1916, in AMNH]. Utah distribution: Alpine. 14 July.

Wilcoxia painteri **Wilcox** 1972b: 43–47 [Holotype: Male, Datil, Continental Divide, Catron Co., New Mexico, 17 July 1930, in Painter Collection?]. Utah distribution: Box Elder Co.: Howell, Nafton, Showell; Emery Co.: east of Block Mtn., Sinbad Country; Garfield Co.: 4 mi N Boulder; Kane Co.: 40 mi E Kanab, 16 mi W Glen Cyn., 3 mi W Wahweep, Zion National Park near east entrance; Millard Co.: 23 mi W Delta: Uintah Co.: 16 mi SW Vernal; Wayne Co.: east edge Capitol Reef. 19 May–16 September.

Willistonina bilineata **(Williston)** 1883: 11 [Holotype: Female, Northern California, in KU]. Utah distribution: Wasatch Co.: Trout Cr. Spring (near Strawberry Reservoir). 20 August.

Subfamily Laphriinae

Atomosia mucida **Osten Sacken** 1887: 184 [Holotype: Sex not known, Presidio, Mexico]. Utah distribution: Washington Co.: Leeds Cyn., Rockville, Santa Clara. 18 July–20 August.

Cerotainiops abdominalis **(Brown)** 1897: 103 [Holotype: information not found]. Utah distribution: Beaver Co.: Milford; Garfield Co.: Escalante Desert, The Hall; Millard Co.: Hatton, Hinckley, Kanosh; San Juan Co.: Bluff; Tooele Co.: Dugway Proving Grounds. 5 June–12 July.

Dasylechia atrox **(Williston)** 1883: 28 [Holotype: Sex not known, Pennsylvania]. Utah distribution: Cache Co.: Logan. No date on label, Utah specimen in AMNH.

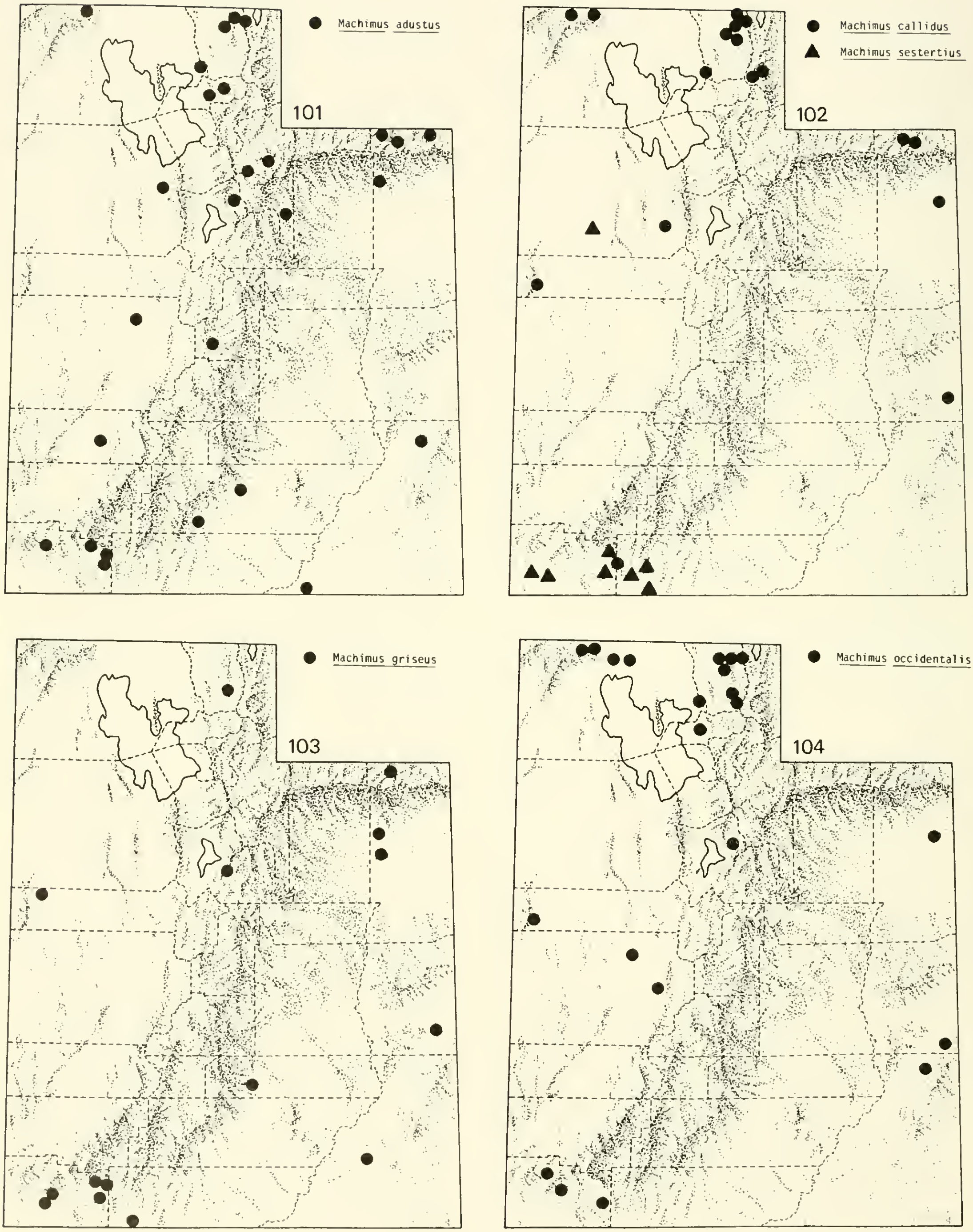
Laphria felis **(Osten Sacken)** 1877: 286 [Holotype: Webber Lake, Sierra Nevada, California, no sex or repository listed in Osten Sacken (1878) or McAtee (1919)]. Utah distribution: Box Elder Co.: Willard Peak; Kane Co.: Duck Lake, Navajo Lake; San Juan Co.: Bear Ears; Summit Co.: Trial Lake; Weber Co.: Ogden, Ogden Peak, Willard Peak. 17 June–3 August.

Laphria fernaldi **(Back)** 1904: 290 [Syntypes: Males and females, Colorado, in either UM or AESP]. Utah distribution: Cache Co.: Green Cyn., Logan, Logan Cyn., Twin Creek; Daggett Co.: Elk Park; Duchesne Co.; Garfield Co.: Bryce Cyn.; Iron Co.: Deer Haven Cmpgd.; Rich Co.: Logan Cyn. summit; San Juan Co.: Bear Ears; Summit Co.: Trial Lake; Uintah Co.: Whiterocks Cyn., Utah Co.: Aspen Grove, Hobble Cr. Cyn., Provo; Washington Co.: Pine Valley, Zion National Park; Wayne Co.: Hanksville. June–September.

Laphria gilva **(Linnaeus)** 1758: 605 [Holotype: Lost]. Utah distribution: Cache Co.: Logan; Garfield Co.: Bryce Cyn. 5 June.

Laphria janus **McAtee** 1919: 153 [Holotype: Male, near summit of Mt. Washington, New Hampshire, in USNM]. Utah distribution: Duchesne Co.: Uinta Mtns.; Garfield Co.: Aquarius Plateau. No dates on labels.

Laphria sadales **Walker** 1849: 378 [Holotype: Sex not known, New York, in British Museum]. Utah distribution: Cache Co.: Green Cyn.; Duchesne Co.: Mirror Lake, Uinta Mtns.; Rich Co.: Logan Cyn. summit, Monte Cristo; Summit Co.: Hole in Rock


● Machimus adustus
101
● Machimus callidus
▲ Machimus sestertius
102
● Machimus griseus
103
● Machimus occidentalis
104

Figs. 101–104. Utah Asilidae, distribution: 101, *Machimus adustus*; 102, *Machimus callidus* and *Machimus sestertius*; 103, *Machimus griseus*; 104, *Machimus occidentalis*.

Cyn.; Uintah Co.; Utah Co.: Aspen Grove, Provo Cyn.; Weber Co.: Pineview. 21 July–16 August.

Laphria vivax **Williston** 1883: 30 [Holotype: Sex not known, Washington Territory, no repository listed in McAtee (1918)]. Utah distribution: Cache Co.: Logan Cyn., Tony Grove; Summit Co.: 3 mi SE Bear River Ranger Station; Wasatch Co.: Silver Lake. 5 August–11 September.

Subfamily Asilinae

Asilus auriannulatus **Hine** 1906 [Syntypes: Male and female, Hope Mtns., B.C., 1 July, no repository listed]. Utah distribution: Cache Co.: Blacksmith Fork Cyn., Green Cyn., Little Bear Cr., Logan, Logan Cyn., Twin Creek, Wellsville; Rich Co.: Logan Cyn. summit. 1–26 July.

Asilus formosus **Hine** 1918: 321 [Holotype: Male, Clary Co., Kansas, 29 August 1911, in the Hine Collection (OSU?)]. Utah distribution: Box Elder Co.: 25 mi SW Snowville; Cache Co.: Petersboro; Millard Co.: Fillmore; Tooele Co.: Lakeside Mtns.; Weber Co.: Huntsville. 10 July–13 August.

Asilus vescus **Hine** 1918: 320 [Holotype: Male, Monterrey Co., California, 2 July 1896, in AMNH]. Utah distribution: Box Elder Co.: Willard Basin; Cache Co.: Blacksmith Fork Cyn.; Daggett Co.: Manila; Millard Co.: Delta; Rich Co.: Randolph. 15 June–1 September.

Efferia aestuans **(Linnaeus)** 1763: 413 [Holotype: Lost]. Utah distribution: Daggett Co.: Manila; Garfield Co.: Bryce Cyn.; Washington Co.: Snow Cyn. 19 May–11 August.

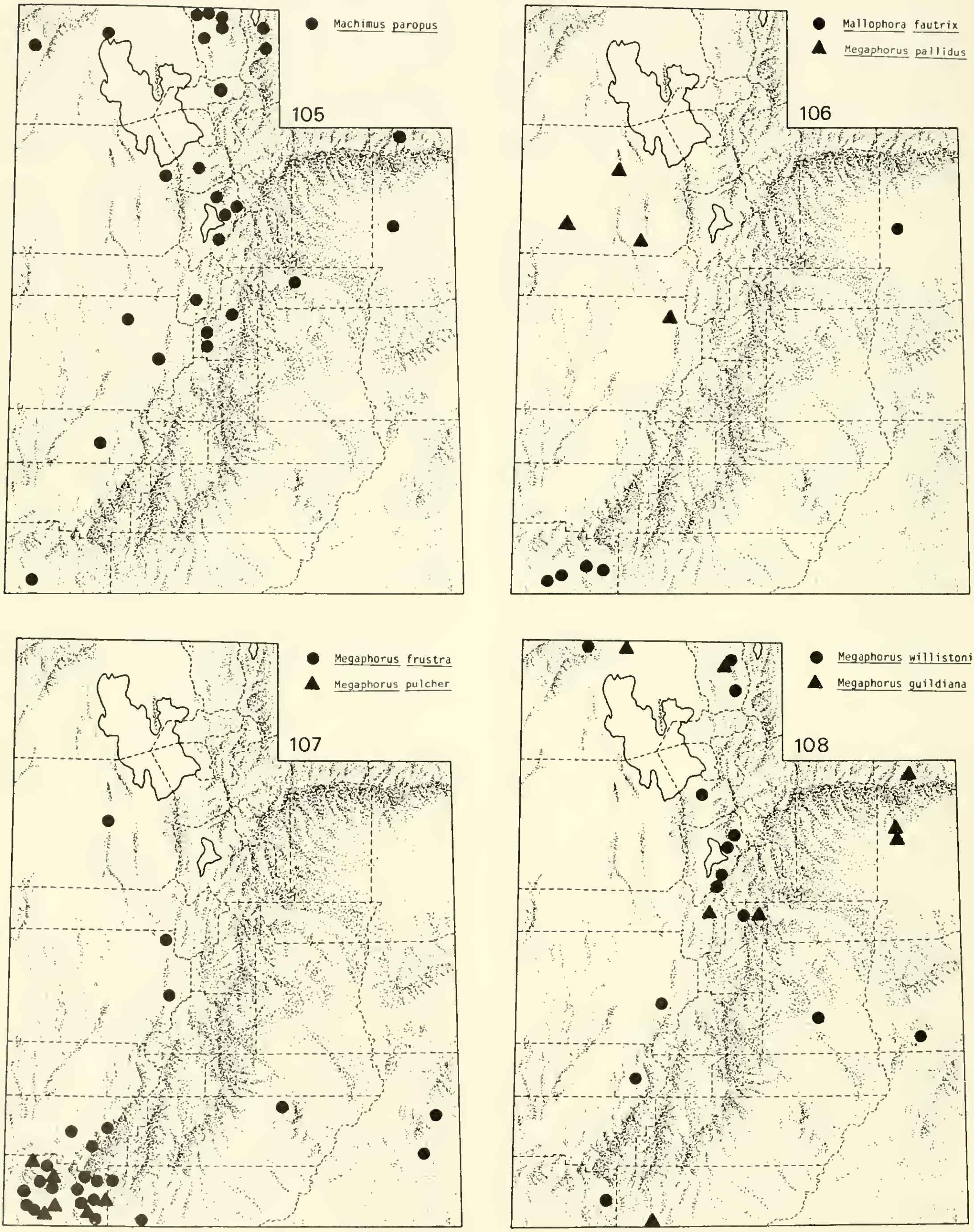
Efferia albibarbis **(Macquart)** 1838: 118 [Holotype: Sex not known, 'North America,' repository not found]. Utah distribution: Cache Co.: Cornish, Logan, Paradise, Wellsville; Duchesne Co.: Myton; Emery Co.: Green River, Woodside; Garfield Co.: Henrieville, Ten Mile (Escalante Desert); Grand Co.: Arches, Castleton, Castle Valley, La Sal Mtns., Moab; Juab Co.: Trout Cr.; Millard Co.: Delta, Fillmore; San Juan Co.: Bluff; Tooele Co.: Little Granite Mtns.; Uintah Co.: Fort Duchesne, Maeser; Utah Co.: east side Utah Lake, Provo; Washington Co.: Leeds, Pinto, Rockville, Santa Clara, Snow Cyn., St. George, Zion National Park—Coalpits Wash, Narrows; Wayne Co.: Notom; Weber Co.: Hooper, Riverdale. 7 May–1 August.

Efferia apache **Wilcox** 1966a: 141 [Holotype: Male, Chambers, Arizona, 18 May 1965, in CAS]. Utah distribution: Emery Co.: 4 mi N Gilson Butte, Goblin Valley, San Rafael Desert, 3 mi SSE Temple Mtn., 5,300 ft; San Juan Co.: Bluff. 16 April–29 May.

Efferia arida **(Williston)** 1893: 254 [Holotype: Male, Death Valley Expedition, April 1891, in USNM]. Utah distribution: Washington Co.: Leeds. 4–23 April.

Efferia basini **Wilcox** 1966a: 190 [Holotype: Male, 28.5 mi W Eureka, Eureka Co., Nevada, 6 June 1960, in CIS]. Utah distribution: Box Elder Co.: Cedar Cr., Snowville; Grand Co.: 12 mi NW Moab; Wayne Co.: Horse Valley. 28 May–19 June.

Efferia benedicti **(Bromley)** 1940: 15 [Holotype: Male, Winslow, Arizona, 13 June 1937, in KU]. Utah distribution: Beaver Co.: Milford, Minersville Reservoir; Box Elder Co.: Clear Cr., Kelton, Lampo Jct., Mantua, Promontory, Raft River Mtns., Rattlesnake Pass, Snowville, Tecoma Range; Cache Co.: Beaver Mtn., Blacksmith Fork Cyn., Dry Cyn., Green Cyn., Logan, Logan Cyn., Providence; Carbon Co.: Carbon Airport, Dragerton, Kennilworth, Price, Woodhill; Davis Co.: Antelope Island, Farmington; Daggett Co.: Bridgeport; Duchesne Co.: Duchesne; Emery Co.: Buckskin Springs, Block Mtn., 4 mi N Gilson Butte, Sinbad Country; Garfield Co.: Boulder, 11 mi E Escalante, Escalante Desert, Halls Cr., Long Hollow, Shitamaring Cyn., Ten Mile, Willow Tanks; Grand Co.: Castle Valley, Moab; Iron Co.: Cedar City, Parowan; Juab Co.: Antelope Springs, Callao, Deep Cr. Mtns., Levan, Thomas Range, Topaz Mtn., Trout Cr., Utah Agricultural Experiment Station north of Levan; Kane Co.: Glendale, Kanab, Kodachrome Basin, Zion National Park; Millard Co.: Confusion Pass, Delta, Fillmore, Flowell, Garrison, Hatton, Oak City, Pahvant, Scipio Lake; Piute Co.: Marysvale; Salt Lake Co.: Dry Cyn., Fort Douglas, Salt Lake City; San Juan Co.: Blanding, Hite, Kane Springs, Lime Cr., Monticello, Bluff, Monument Valley, Natural Bridges National Monument, Navajo Mtn. Trading Post; Sanpete Co.: 8 mi NE Fountain Green; Sevier Co.: Fish Lake, Fremont Jct., Gooseberry, Richfield; Tooele Co.: Cedar Mtns., Clifton, Delle, Dugway Mtns., between Johnson and Douglas passes, Lookout Mountain, Skull Valley, Simpson Springs,


● Machimus paropus
105
● Mallophora fautrix
▲ Megaphorus pallidus
106
● Megaphorus frustra
▲ Megaphorus pulcher
107
● Megaphorus willistoni
▲ Megaphorus guildiana
108

Figs. 105–108. Utah Asilidae, distribution: 105, *Machimus paropus*; 106, *Mallophora fautrix* and *Megaphorus pallidus*; 107, *Megaphorus frustra* and *Megaphorus pulcher*; 108, *Megaphorus willistoni* and *Megaphorus guildiana*.

Stansbury Island, Timpie, Wendover; Uintah Co.: Dinosaur National Monument, Evacuation Cr., Vernal; Utah Co.: Alpine, Aspen Grove, Cedar Valley, Goshen, Oquirrh Mtns., Payson, Provo, Rock Cyn., Spanish Fork, West Cyn., west Utah Lake, Y Mtn.; Washington Co.: Beaver Dam Mtns., Dixie National Forest, Hurricane, Ivins, Leeds Cyn., St. George, Summit, Toquerville, Veyo, Zion National Park; Wayne Co.: Experiment Station, Fruita, Grover, Hanksville, Notom, Torrey, 6 mi W Torrey; Weber Co.: Farr West, North Ogden, Ogden. 23 April–28 August.

Efferia bicolor **(Bellardi)** 1861: 47 [Holotype: Male, 'Mexico,' repository not listed in Wilcox (1966)]. Utah distribution: Box Elder Co.: Kelton; Cache Co.: Logan; Daggett Co.: Bridgeport, Hideout Cyn.; Iron Co.: Cedar City; Juab Co.: Trout Cr.; Washington Co.: Zion National Park. 19 July–24 July.

Efferia cana **(Hine)** 1916: 22 [Syntypes: Males and females, Claremont, California, in OSU]. Utah distribution: Juab Co.: Fish Springs; Kane Co.: Wahweep Va.; Millard Co.: Delta; Utah Co.: Provo; Washington Co.: 15 mi SW Shivwits, Hurricane, La Verkin, Leeds, Pintura, Santa Clara, St. George, 3 mi N St. George; Wayne Co.: Hanksville. 23 April–1 June.

Efferia costalis **(Williston)** 1885: 64 [Holotype: None listed]. Utah distribution: Box Elder Co.: Curlew Valley; Cache Co.: Franklin Basin; Carbon Co.: Price; Daggett Co.: Elk Park; Duchesne Co.: Yellowstone Ranger Station; Garfield Co.: Bryce Cyn., Daves Hollow, Panguitch Lake; Iron Co.: Kanarraville; Kane Co.: Coral Pink Sand Dunes; Millard Co.: Antelope Mtn.; Rich Co.: Sage Cr. Jct.; Salt Lake Co.: Parleys Cyn.; San Juan Co.: Blanding; Tooele Co.: James Ranch—Government Spring; Washington Co.: New Harmony. 9 June–7 August.

Efferia davisi **Wilcox** 1966a: 132 [Holotype: Male, 12 mi N Sasabe, Arizona, 5 August 1962, in CAS]. Utah distribution: Washington Co.: Ivins, Leeds, Rockville, Santa Clara, Zion National Park. 15–19 July.

Efferia deserti **Wilcox** 1966a: 199 [Holotype: Male, 10 mi E Desert Center, California, 13 April 1941, in CAS]. Utah distribution: Washington Co.: Santa Clara, St. George, Zion National Park. 4–15 May.

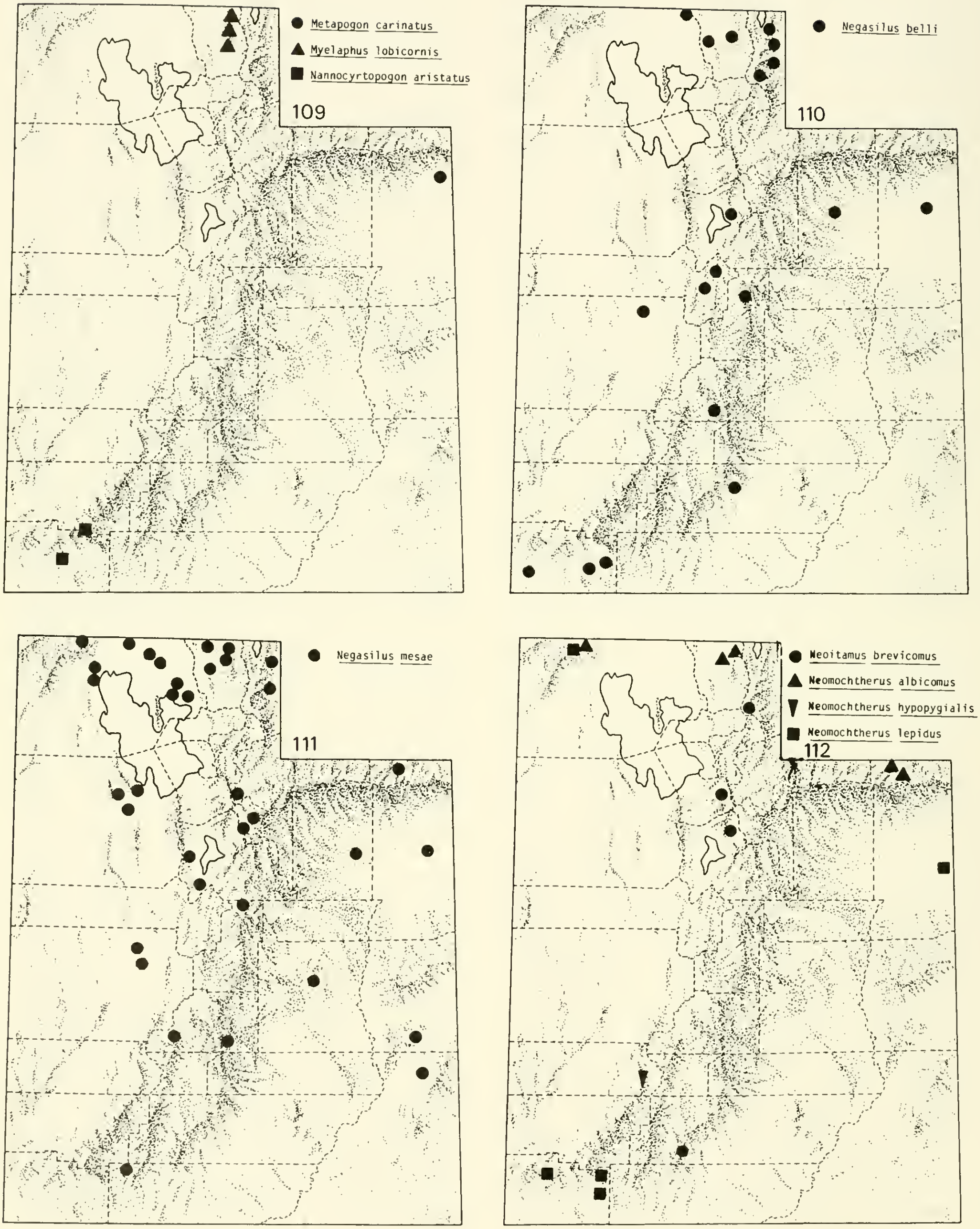
Efferia frewingi **Wilcox** 1966a: 169 [Holotype: Male, Antelope Mtn., Harney Co., Oregon, 6,500 ft, 9 August 1931, in CAS]. Utah distribution: Box Elder Co.: Clear Cr., Kelton Pass, Promontory, Yost; Cache Co.: Logan; Daggett Co.: Dutch John, Hideout Cyn., Manila; Duchesne Co.: Duchesne, Monarch, Myton, Roosevelt, 10 mi N Neola; Emery Co.: Buckhorn Flats, fossil beds, Green River, Gilson Butte; Garfield Co.: Henrieville, Henry Mtns.; Juab Co.: Eureka, Topaz; Kane Co.: Zion National Park—Chamberlain Ranch; Millard Co.: Fillmore, Desert Experiment Station; Sanpete Co.: 8 mi NE Fountain Green; Sevier Co.: Richfield; Tooele Co.: Clifton, Little Granite Mountain; Uintah Co.: Diamond Mtn., Dinosaur National Monument, Jensen, Red Wash, Vernal; Utah Co.: Alpine, Goshen, Provo, west Utah Lake; Wasatch Co.: Strawberry Valley; Washington Co.: Crystal Cr., Hurricane, Leeds, Pintura. 26 July–8 September.

Efferia knowltoni **(Bromley)** 1937b: 104 [Syntypes: Male and female, Trout Creek, Utah, 5–6 1934, in USU or USNM (not seen at USU)]. Remarks: A specimen labeled Trout Creek, Utah, 5–6 1934 but without a type label in the USU collection was examined, and it ran to *Efferia benedicti* in the Wilcox (1966a) key. No male specimens examined during this study, including numerous specimens from Trout Creek, ran to this species in the key. Some females do indeed run to this species based on the position of the fork of the third vein (in the Wilcox key). Upon closer observation this character was found variable in the specimens, even in those from the same locality. Therefore, status of this species should be that of synonomy under *E. benedicti* until characters separating this species can be found.

Efferia mortensoni **Wilcox** 1966a: 173 [Holotype: Male, 2 mi NE Portal, Arizona, 23 October 1962, in CAS]. Utah distribution: Snow Cyn., St. George. 7 October.

Efferia pernicus **Coquillett** 1893: 175 [Syntypes: Male and female, Los Angeles and San Diego counties, California, in USNM]. Utah distribution: Kane Co.: Zion National Park—Chamberlain Ranch; Washington Co.: Boilers in Washington, Rockville—Duncan Flats. 29 July–5 September.

Efferia producta **(Hine)** 1919: 136 [Syntypes: Male and female, Flinn Springs, Lakeside, California, 9 August 1917, in OSU].


● Metapogon carinatus
▲ Myelaphus lobicornis
■ Nannocyrtopogon aristatus
109
● Negasilus belli
110
● Negasilus mesae
111
● Neoitamus brevicomus
▲ Neomochtherus albicomus
▼ Neomochtherus hypopygialis
■ Neomochtherus lepidus
112

Figs. 109–112. Utah Asilidae, distribution: 109, *Metapogon carinatus*, *Myelaphus lobicornis*, and *Nannocyrtopogon aristatus*; 110, *Negasilus belli*; 111, *Negasilus mesae*; 112, *Neoitamus brevicomus*, *Neomochtherus albicomus*, *Neomochtherus hypopygialis*, and *Neomochtherus lepidus*.

Utah distribution: Kane Co.: Kanab; San Juan Co.: Navajo Mtn.; Washington Co.: Zion National Park. 17 July–28 August.

Efferia staminea **(Williston)** 1885: 68 [Holotype: Male, Montana, in KU]. Utah distribution: Daggett Co.: Pipe Creek. 6 August.

Efferia subarida **(Bromley)** 1940: 14 [Holotype: Types—male and female, Tucson, Arizona, 8 March 1937, in KU]. Utah distribution: Garfield Co.: Shitamaring Cyn. 18 May.

Efferia subcuprea **(Schaeffer)** 1916: 66 [Holotype: Male, Prescott, Arizona, in USNM]. Utah distribution: Beaver Co.: Beaver: Box Elder Co.: Willard Basin; Garfield Co.: Aquarius Plateau; Grand Co.: Moab; Iron Co.: Parowan; Kane Co.: Paria River; San Juan Co.: Kane Springs; Tooele Co.: Little Granite Mtn.; Utah Co.: Provo Cyn.; Washington Co.: Zion National Park. 29 June–29 August.

Efferia subpilosa **(Schaeffer)** 1916: 67 [Holotype: Male, Beaver Creek Hills, Beaver Co., Utah, in USNM]. Remarks: Wilcox (1966a) sensed problems with respect to the identity of this species. Apparently no specimens which he studied could confidently be placed in this species. I have not seen any specimens which would fit the descriptions outlined by the Wilcox (1966a) key. The type should be examined to determine the status of this species.

Efferia tucsoni **Wilcox** 1966a: 231 [Holotype: Male, Portal, Arizona, 23 July 1963, in CAS]. Utah distribution: Garfield Co.: Shitamaring Cyn.; San Juan Co.: Natural Bridges National Monument; Washington Co.: Leeds Cyn., Paradise Cyn. (near Ivins), Santa Clara, Zion National Park. 14–27 July.

Efferia utahensis **(Bromley)** 1937b: 103 [Holotype: Male, Price, Utah, 26 August 1935, in USU or USNM (not seen at USU)]. Utah distribution: Carbon Co.: 1 mi S Price; Emery Co.: 2 air mi W Little Gilson Butte, Goblin Valley (in wash), 4 air mi N Gilson Butte; Garfield Co.: Henry Mtns., Wickiup Pass; Grand Co.: Westwater; San Juan Co.: 8 mi NE Mexican Hat. 15 August–17 September.

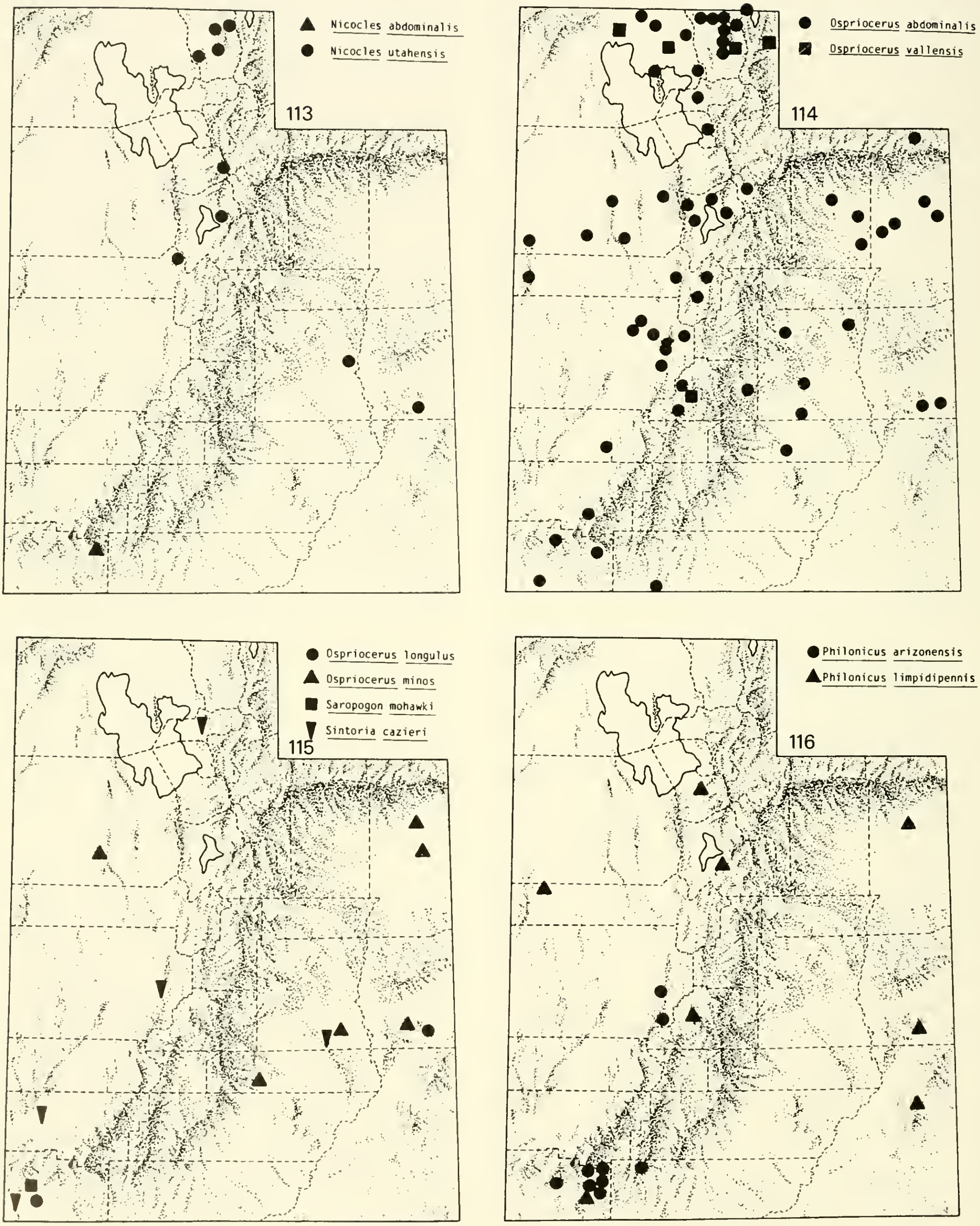
Efferia willistoni **(Hine)** 1919: 110 [Syntypes: Male and female, Williams, Arizona, 21 July, in USNM]. Utah distribution: Cache Co.: Green Cyn., Logan Cyn.; Grand Co.: Castleton, La Sal Mtns.; Millard Co.: Cove Fort, Fillmore; Salt Lake Co.: Magna, Salt Lake City; San Juan Co.: Grand Gulch, Natural Bridges National Monument; Washington Co.: Crystal Cr., Deep Cr., Leeds Cyn., Zion National Park—Court of the Patriarchs, Oak Cr. 6 May–6 August.

Efferia zonata **(Hine)** 1919: 112 [Syntypes: Male and female, southern Arizona, August 1902, in OSU]. Utah distribution: Box Elder Co.: Clear Cr., 5 mi N Kelton, Mantua; Cache Co.: Blacksmith Fork Cyn., Dry Cyn., Green Cyn., Hatties Grove, Logan, Providence Cyn.; Daggett Co.: 14 mi S Manila; Emery Co.: San Rafael Reef, S. Temple Wash; Garfield Co.: Henrieville; Juab Co.: Antelope Springs; Millard Co.: Delta, Fillmore, Gandy; San Juan Co.: Hite; Sanpete Co.: Ephraim; Tooele Co.: Deep Cr. Mtns., Hickman Cyn., Johnson Pass, Mercur, Whiskey Springs; Utah Co.: Payson, Provo; Washington Co.: Leeds, Snow Cyn., Zion National Park. 30 June–28 August.

Machimus adustus **Martin** 1975: 27 [Holotype: Male, White Mtns., Bee Hive Springs, Arizona, 18 July 1949, in CAS]. Utah distribution: Beaver Co.: Milford; Box Elder Co.: Clear Cr., Mantua; Cache Co.: Green Cyn., Logan, Logan Cyn., Tony Grove, Twin Cr., West Hodges Cyn.; Daggett Co.: 4 mi E Deep Cr., Pipe Creek Summit Ranger Station; Garfield Co.: Boulder, Bryce Cyn.; Millard Co.: Delta; Rich Co.: Garden City, Logan Cyn. summit; San Juan Co.: Kane Springs, Navajo Mtn.; Sanpete Co.: Centerfield; Summit Co.: 16 mi '?' Kamas; Tooele Co.: Tooele; Uintah Co.: Whiterocks Cyn.; Utah Co.: Aspen Grove; Wasatch Co.: Keetley, Strawberry Reservoir; Washington Co.: Kolob, Pine Valley, Zion National Park—East Rim, Lava Point; Weber Co.: Huntsville, Uintah. 20 June–18 September.

Machimus callidus **Williston** 1893: 75 [Syntypes: Male and female, Mt. Hood, in KU]. Utah distribution: Box Elder Co.: Clear Cr., Willard Basin, Yost; Cache Co.: Blacksmith Fork Cyn., Franklin Basin, Green Cyn., Logan, Logan Cyn., Providence, Tony Grove, White Pine Lake; Daggett Co.: Hideout Cyn., Manila; Grand Co.: Castle Valley; Juab Co.: Trout Cr.; Rich Co.: Logan Cyn. summit, Monte Cristo, Walton (Allen) Cyn.; Tooele Co.: Vernon; Uintah Co.: Jensen; Washington Co.: Zion National Park. 6 May–10 September.

Machimus griseus **Hine** 1906: 29 [Syntypes:


▲ Nicocles abdominalis
● Nicocles utahensis
113
● Ospriocerus abdominalis
■ Ospriocerus vallensis
114
● Ospriocerus longulus
▲ Ospriocerus minos
■ Saropogon mohawki
▼ Sintoria cazieri
115
● Philonicus arizonensis
▲ Philonicus limpidipennis
116

Figs. 113–116. Utah Asilidae, distribution: 113, *Nicocles abdominalis* and *Nicocles utahensis*; 114, *Ospriocerus abdominalis* and *Ospriocerus vallensis*; 115, *Ospriocerus longulus*, *Ospriocerus minos*, *Saropogon mohawki*, and *Sintoria cazieri*; 116, *Philonicus arizonensis* and *Philonicus limpidipennis*.

Male and female, 'Southwestern Colorado,' no repository listed]. Utah distribution: Cache Co.: Blacksmith Fork Cyn.; Daggett Co.: Manila; Grand Co.: Castleton; Juab Co.: Callao; Kane Co.: Kanab; San Juan Co.: Natural Bridges National Monument; Uintah Co.: Fort Duchesne, Whiterocks; Utah Co.: Hobble Cr. Cyn.; Washington Co.: Boilers—Washington, Crystal Cr., Deep Cr., Leeds, Zion National Park—Court of the Patriarchs; Wayne Co.: Grover. 10 July–12 September.

Machimus occidentalis **(Hine)** 1909: 147 [Type: None designated, several specimens, noted by Hine (1909) from B.C., Nevada, California, Oregon, and Washington]. Utah distribution: Box Elder Co.: Clear Cr., Curlew Valley, Hansel Valley, Mantua, Raft River Mtns.; Cache Co.: Ant Valley, Blacksmith Fork Cyn., Green Cyn., Logan Cyn., Providence, Tony Grove, Twin Creek; Grand Co.: La Sal Mtns.; Juab Co.: Trout Cr.; Millard Co.: Delta, Holden; Rich Co.: Logan Cyn. summit; San Juan Co.: 25 mi S Moab; Uintah Co.: Jensen; Utah Co.: South Fork of Provo Cyn.; Washington Co.: Leeds, Pine Valley, Zion National Park; Weber Co.: Ogden. 3 June–25 July.

Machimus paropus **(Walker)** 1849: 455 [Holotype: Not listed in Hine (1909)]. Utah distribution: Beaver Co.: Milford; Box Elder Co.: Grouse Cr., 25 mi SW Snowville; Cache Co.: Clarkston, Cornish, Mendon, Petersboro, Richmond, Smithfield Cyn.; Carbon Co.: Helper; Daggett Co.: Manila; Juab Co.: Chicken Cr. Reservoir; Millard Co.: Delta, Fillmore; Rich Co.: Laketown, Randolph; Salt Lake Co.: Midvale; Sanpete Co.: Centerfield, Ephraim, Fayette, Sanpete; Tooele Co.: Mills Jct.; Uintah Co.: Fort Duchesne; Utah Co.: American Fork, Provo, South Fork of Provo Cyn., Spanish Fork; Washington Co.: St. George; Weber Co.: Huntsville. 6 May–2 September.

Machimus sestertius **Martin** 1975: 29 [Holotype: Male, 4.5 mi E Moenkopi, Coconino Co., Arizona, 14 July 1966, in CAS]. Utah distribution: Kane Co.: Coral Pink Sand Dunes, Kanab, 10 mi N Kanab; Tooele Co.: Dugway Proving Grounds; Washington Co.: Crystal Cr., Deep Cr., Santa Clara, St. George, Zion National Park. 13 May–21 September.

Mallophora fautrix **Osten Sacken** 1877: 191 [Holotype: Presidio, Mexico, no sex or repository listed]. Utah distribution: Uintah Co.: Randlett (?); Washington Co.: La Verkin, St. George, Washington, Zion National Park. 4 July–15 August.

Megaphorus frustra **(Pritchard)** 1935: 11 [Holotype: Male, Tem (south of Whitewater), Arizona, 19 August 1934, in AMNH]. Utah distribution: Garfield Co.: Cass Cr. Reservoir; Iron Co.: Cedar City, Iron Springs, Parowan; Kane Co.: Kanab; Millard Co.: Chalk Cr., Leamington; San Juan Co.: Blanding, Monticello; Tooele Co.: Cedar Mtns.; Washington Co.: Anderson Jct., Ash Cr., Gunlock, Leeds Cyn., Little Pinto, Pintura, Utah State Line U 59, Zion National Park. 14 June–26 August.

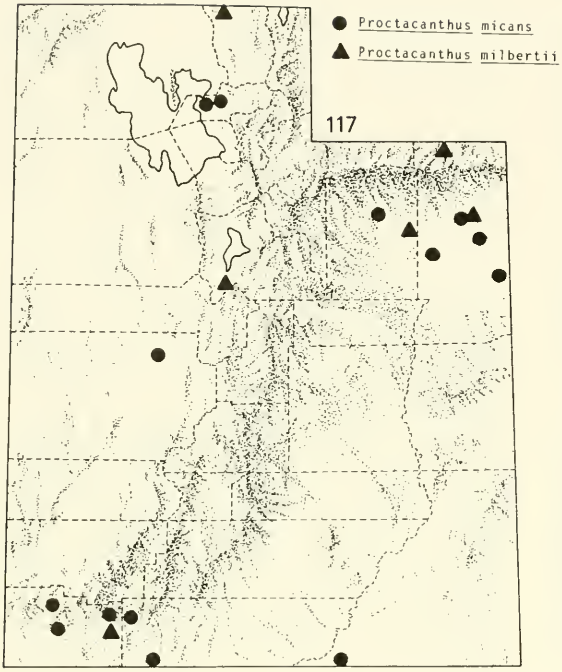
Megaphorus guildiana **(Williston)** 1885: 60 [Types: western Kansas, Montana, North Carolina, in KU]. Utah distribution: Box Elder Co.: Snowville; Cache Co.: Green Cyn., Logan; Daggett Co.: Forest Camp, Hideout Cyn.; Juab Co.: Nephi; Kane Co.: Kanab; Sanpete Co.: Fairview; Uintah Co.: La Point, Tridell. 5–23 August.

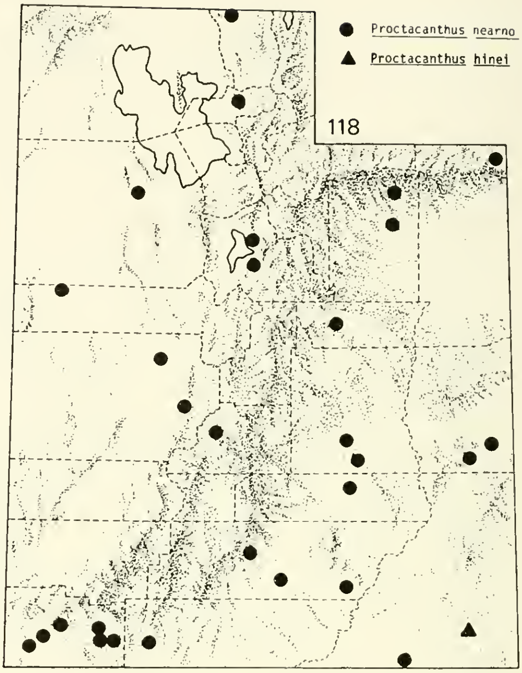
Megaphorus pallidus **(Johnson)** 1958: 41 [Holotype: Male, west side of Little Granite Mtn., Tooele Co., Utah, 21 August 1955; in Johnson collection (paratypes seen at BYU)]. Utah distribution: Millard Co.: 9 mi E Delta; Tooele Co.: Cedar Mtns., Hickman Cyn., Simpson Mtns., west side of Little Granite Mtn. 23 July–21 August.

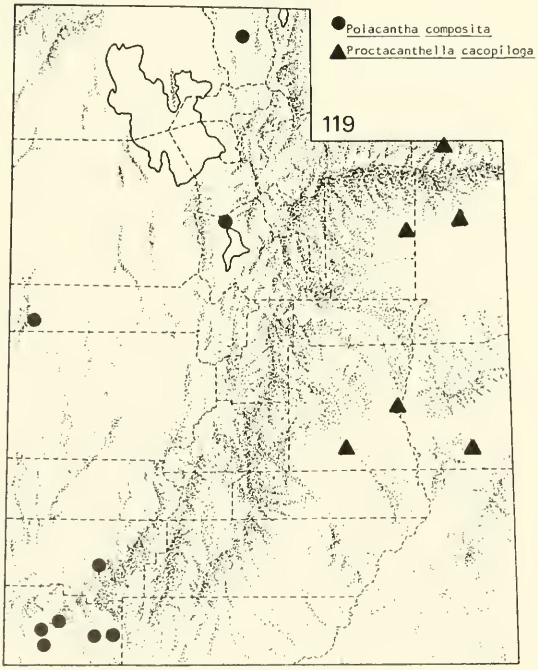
Megaphorus pulcher **(Pritchard)** 1935: 11 [Holotype: Carlsbad, New Mexico, 29 August 1934, in AMNH]. Utah distribution: Washington Co.: Enterprise, Middleton, Pine Valley, Rockville, St. George, Zion National Park. 10 August–14 October.

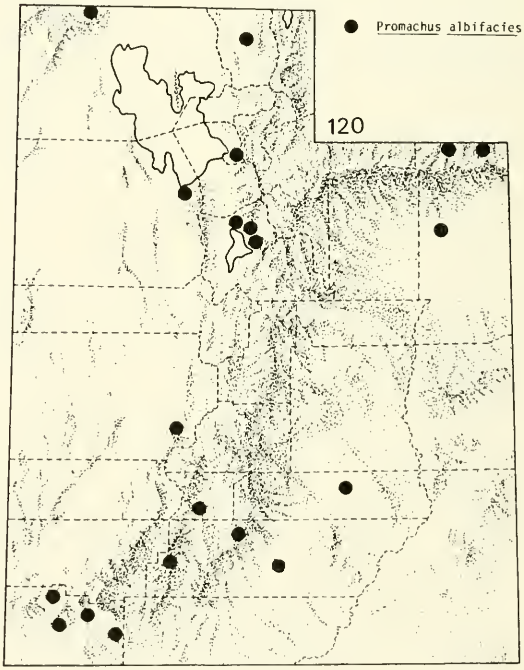
Megaphorus willistoni (Cole,) *in* Cole and Pritchard 1964: 74 [Holotype: Male, Hallelujah Jct., Lassen Co., California, 26 July, in CAS]. Utah distribution: Beaver Co.: Beaver; Box Elder Co.: Clear Cr.; Cache Co.: Blacksmith Fork Cyn., Green Cyn., Logan; Emery Co.: Block Mtn., Sinbad Country; Grand Co.: Moab; Millard Co.: Fillmore; Salt Lake Co.: Salt Lake City; Sanpete Co.: 8 mi NE Fountain Green; Utah Co.: BYU, Provo, Rock Cyn., Spanish Fork, Spring Lake; Washington Co.: Zion National Park. 8–24 August.

Negasilus belli **Curran** 1934: 184 [Holotype: None listed]. Utah distribution: Box Elder Co.: Portage; Cache Co.: Logan, Mendon; Duchesne Co.: Duchesne; Garfield Co.:


● Proctacanthus micans
▲ Proctacanthus milbertii
117


● Proctacanthus nearno
▲ Proctacanthus hinei
118


● Polacantha composita
▲ Proctacanthella cacopiloga
119


● Promachus albifacies
120

Figs. 117–120. Utah Asilidae, distribution: 117, *Proctacanthus micans* and *Proctacanthus milbertii*; 118, *Proctacanthus nearno* and *Proctacanthus hinei*; 119, *Polacantha composita* and *Proctacanthella cacopiloga*; 120, *Promachus albifacies*.

Boulder; Juab Co.: Chicken Cr., Nephi; Millard Co.: Delta; Rich Co.: Laketown, Randolph, Walton (Allen) Cyn., Woodruff; Sanpete Co.: Fairview; Sevier Co.: Koosharem Reservoir; Uintah Co.: Vernal; Utah Co.: Provo; Washington Co.: Santa Clara, Virgin, Zion National Park. 13 June–23 July.

Negasilus mesae **(Tucker)** 1907: 51 [Holotype: Colorado Springs, Colorado, in KU]. Utah distribution: Box Elder Co.: Bird Refuge, Blue Cr., Brigham City, Corinne, Howell, Kelton, Locomotive Springs, Nafton, Snowville; Cache Co.: Beaver Mtn., Benson, Cornish, Logan Cyn.—Twin Cr.; Daggett Co.: Manila; Duchesne Co.: Myton; Emery Co.: 9 air mi E Castledale, Sinbad Country east of Block Mtn.; Grand Co.: Moab; Kane Co.: Navajo Lake; Millard Co.: Delta, Pahvant; Rich Co.: Sage Cr. Jct., Woodruff; San Juan Co.: Kane Springs; Sanpete Co.: Indianola; Sevier Co.: Fish Lake, Sevier; Summit Co.: Park City; Tooele Co.: Delle, Iosepa, Timpie; Uintah Co.: Jensen; Utah Co.: Elberta, Fairfield; Wasatch Co.: Heber, Provo Cyn. 18 May–12 August.

Neoitamus brevicomus **(Hine)** 1909: 155 [Syntypes: Male and female, Kalso, B.C., repository not listed]. Utah distribution: Garfield Co.: Long Hollow; Rich Co.: Monte Cristo; Salt Lake Co.: Mill Creek Ranger Station; Utah Co.: Aspen Grove. 12 July–11 August.

Neomochtherus albicomus **(Hine)** 1909: 136 [Syntypes: Male and female, Montana, in USNM]. Utah distribution: Box Elder Co.: Clear Cr.; Cache Co.: Green Cyn., Twin Cr.; Daggett Co.: Hideout Cyn., Manila. 19 July–4 September.

Neomochtherus hypopygialis **(Schaeffer)** 1916: 68 [Syntypes: Two males, Beaver Cyn., Utah, in AMNH]. Remarks: No specimens of this species were seen in collections during this study.

Neomochtherus lepidus **(Hine)** 1909: 136 [Holotype: Male, Colorado, also female, White Mtns. of New Mexico about 6,000 ft, 23 July, in USNM]. Utah distribution: Box Elder Co.: Clear Cr.; Uintah Co.: Bonanza; Washington Co.: Pine Valley, Zion National Park. 24 August.

Philonicus arizonensis **(Williston)** 1893: 76 [Holotype: Female, Arizona, in KU]. Utah distribution: Kane Co.: Long Valley; Millard Co.: Fillmore, Kanosh Cyn.; Washington Co.: Crystal Cr., Deep Cr., Leeds Cyn., Rockville, Zion National Park—Birch Cr., Coalpits Wash, Court of the Patriarch, Narrows, Taylor Cr. 17 June–28 August.

Philonicus limpidipennis **(Hine)** 1909: 167 [Syntypes: Male and female, southwestern Colorado, 14 July 1899, repository not listed]. Utah distribution: Grand Co.: Moab; Juab Co.: Callao; Salt Lake Co.: Salt Lake City; San Juan Co.: Indian Cr.; Sevier Co.: Richfield; Uintah Co.: Vernal Refuge; Utah Co.: Spanish Fork; Washington Co.: Rockville. 18 June–30 August.

Polacantha composita **(Hine)** 1918: 321 [Holotype: Male, San Diego, California, 30 June 1913, in Hine Collection]. Utah distribution: Cache Co.: Logan; Iron Co.: Cedar City; Juab Co.: Trout Cr.; Utah Co.: Saratoga; Washington Co.: Leeds, Leeds Cyn., Paradise Cyn., St. George, Virgin, Zion National Park. 27 June–28 August.

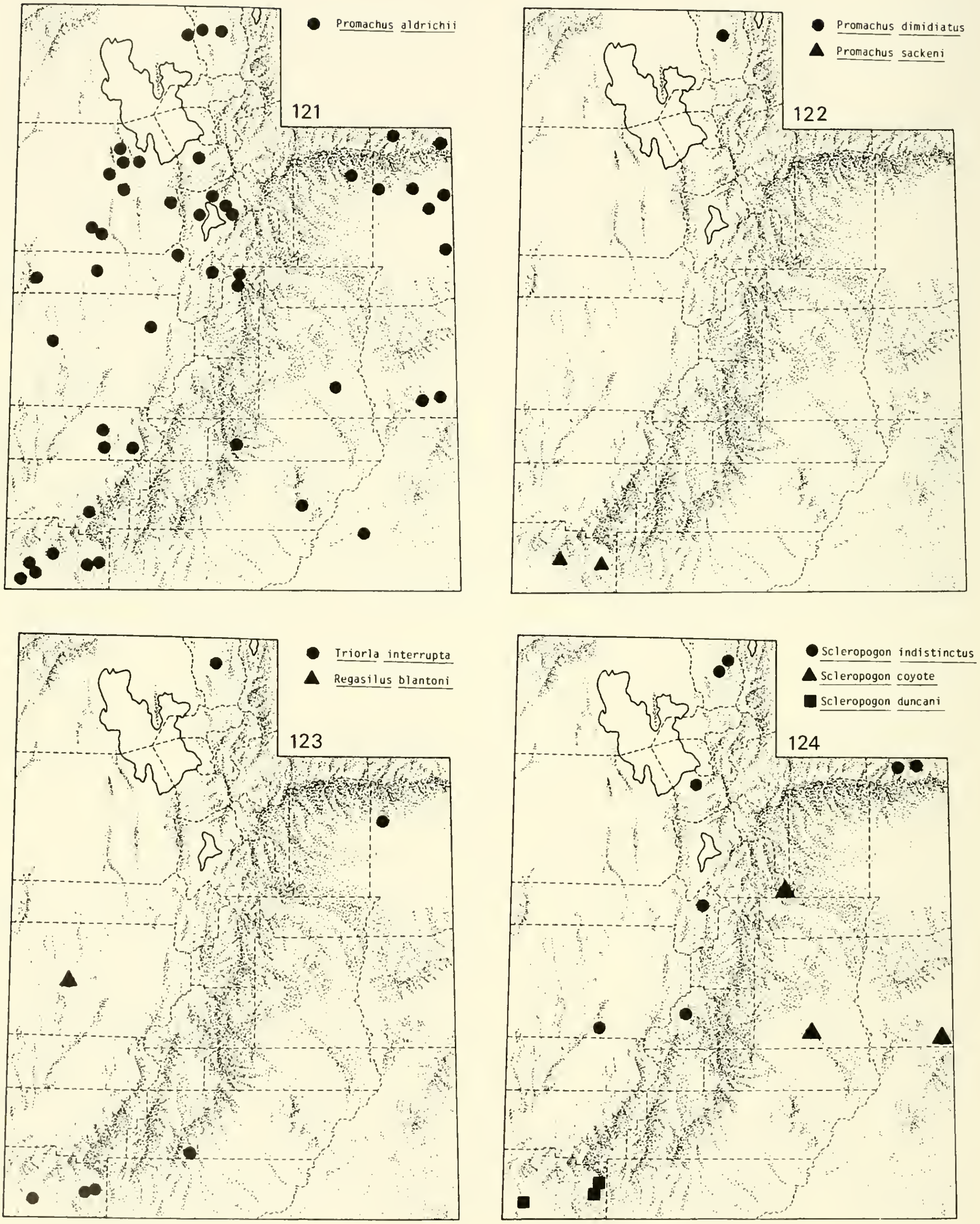
Proctacanthella cacopiloga **(Hine)** 1909: 65 [Syntypes: Several specimens from many states, see Hine (1909), in KU]. Utah distribution: Daggett Co.: Manila; Duchesne Co.: Roosevelt; Emery Co.: Green River, Wild Horse Cr. north of Goblin Valley; Grand Co.: 12 mi NW Moab; Uintah Co.: Vernal. 6 June–16 August.

Proctacanthus hinei **Bromley** 1928: 13 [Holotype: male, Albuquerque, New Mexico, 3 August 1925, S. W. Bromley., in Bromley Collection]. Utah distribution: San Juan Co.: Sand Island Cmpgd. 2 mi S Bluff. 22–23 August.

Proctacanthus micans **Schiner** 1867: 397 [Holotype: None listed in Hine (1911)]. Utah distribution: Duchesne Co.: Boneta; Kane Co.: Kanab, Zion National Park; Millard Co.: Delta; San Juan Co.: Navajo Mtn.; Uintah Co.: Bonanza, Fort Duchesne, Jensen, Vernal; Washington Co.: Leeds Cyn., Pine Valley Cmpg, Zion National Park; Wayne Co.; Weber Co.: Farr West, Ogden. 15 July–19 August.

Proctacanthus milberti **Macquart** 1838: 124 [Holotype: None listed in Hine (1911)]. Utah distribution: Cache Co.: Cornish; Daggett Co.: Manila; Duchesne Co.: Roosevelt; Uintah Co.: Vernal; Utah Co.: Goshen; Washington Co.: Zion National Park. 27 June–11 August.

Proctacanthus nearno **Martin** 1962: 187 [Holotype: Male, Baboquivari Mtns., Ari-



● Promachus aldrichii
121
● Promachus dimidiatus
▲ Promachus sackeni
122
● Triorla interrupta
▲ Regasilus blantoni
123
● Scleropogon indistinctus
▲ Scleropogon coyote
■ Scleropogon duncani
124

Figs. 121–124. Utah Asilidae, distribution: 121, *Promachus aldrichii*; 122, *Promachus dimidiatus* and *Promachus sackeni*; 123, *Triorla interrupta* and *Regasilus blantoni*; 124, *Scleropogon indistinctus*, *Scleropogon coyote*, and *Scleropogon duncani*.

zona, 19 July 1950, in KU]. Utah distribution: Cache Co.: Cornish; Carbon Co.: Price; Daggett Co.: Bridgeport; Duchesne Co.: Bluebell, Uintah Cyn.; Emery Co.: Wildhorse Cr. north of Goblin Valley, 4 mi N Gilson Butte, 2 mi E Little Gilson Butte; Garfield Co.: Boulder, Ten Mile, The Halls; Grand Co.: Castleton, Moab; Juab Co.: Callao; Kane Co.: Coral Pink Sand Dunes; Millard Co.: Delta, Fillmore; San Juan Co.: Goulding; Sevier Co.: Richfield; Tooele Co.: Skull Valley; Utah Co.: Provo, Spanish Fork; Washington Co.: Duncan Flats near Rockville, Leeds Cyn., Middleton, Rockville, Santa Clara, Shunesburg, Zion National Park—Coalpits Wash; Wayne Co.: Hanksville; Weber Co.: Ogden Cyn. 19 July–5 September.

Promachus albifacies **Williston** 1885: 63 [Holotype: Sex not known, Arizona, in KU]. Utah distribution: Box Elder.: Clear Cr. Cyn.; Cache Co.: Logan; Daggett Co.: Pipe Cr., Manila; Davis Co.: Wasatch Forest boundary near Bountiful; Garfield Co.: Aquarius Plateau, Escalante, Panguitch; Millard Co.: Kanosh Cyn.; Piute Co.: Junction; Tooele Co.: Lake Point; Uintah Co.: La Point; Utah Co.: American Fork, Lehi, Provo; Washington Co.: Ash Cr. bridge, Leeds Cyn., Pinto, Zion National Park; Wayne Co.: Hanksville. 10 June–11 August.

Promachus aldrichii **Hine** 1911: 171 [Syntypes: Male and female, Utah, repository not listed, probably in Hine Collection or OSU]. Utah distribution: Beaver Co.: Beaver, Milford, Minersville Reservoir; Box Elder Co.: Collinston; Cache Co.: Logan, Petersboro; Daggett Co.: Bridgeport, Manila; Duchesne Co.: 10 mi N Neola; Emery Co.: Paige Flat, Sinbad Country; Grand Co.: Castle Valley, Moab; Iron Co.: Cedar City; Juab Co.: Eureka, Nephi, Topaz Mtn., Trout Cr.; Kane Co.: Escalante Desert, Willow Tank; Millard Co.: Confusion Pass, Desert Research Station, Pahvant; Salt Lake Co.: Hunter; San Juan Co.: Piute Pass near Grand Gulch; Sanpete Co.: 8 mi NE Fountain Green, Fairview; Tooele Co.: Cedar Mtns., Delle, Dugway Proving Grounds, Flux, Hickman Cyn., Indian Springs, Mercur, Skull Valley, Whiskey Springs; Uintah Co.: Bonanza, Dinosaur National Monument, Jensen, Vernal, Whiterocks; Utah Co.: Lehi, Orem, Rock Cyn., west Utah Lake; Washington Co.: Beaver Dam Mtns., Leeds, old airport, Paradise Cyn., Rockville, St. George, Washington, Zion National Park; Wayne Co.: Teasdale. 8 June–17 September.

Promachus dimidiatus **Curran** 1927: 87 [Holotype: Male, Aweme, Manitoba, July 1920, in CNC]. Utah distribution: Cache Co.: Logan. 4–20 July.

Promachus sackeni **Hine** 1911: 166 [Syntypes: Male and female, southern Arizona, July and August, no repository listed]. Utah distribution: Washington Co.: Leeds Cyn., Zion National Park. 4–20 July.

Regasilus blantoni **Bromley** 1951: 35 [Holotype: Male, Wills (Wells?), Nevada, 19 August 1939, in Bromley Collection]. Utah distribution: Millard Co.: Skull Rock Pass; Washington Co.: Beaver Dam slope near Arizona border. 10 September–8 October.

Triorla interrupta **(Macquart)** 1834: 310 [Holotype: Georgia, location unknown]. Utah distribution: Cache Co.: Cornish, Logan; Garfield Co.: Bryce Cyn.; Uintah Co.: Whiterocks; Washington Co.: Rockville—Duncan Flats, confluence East and North forks Virgin River, St. George. 10 July–11 August.

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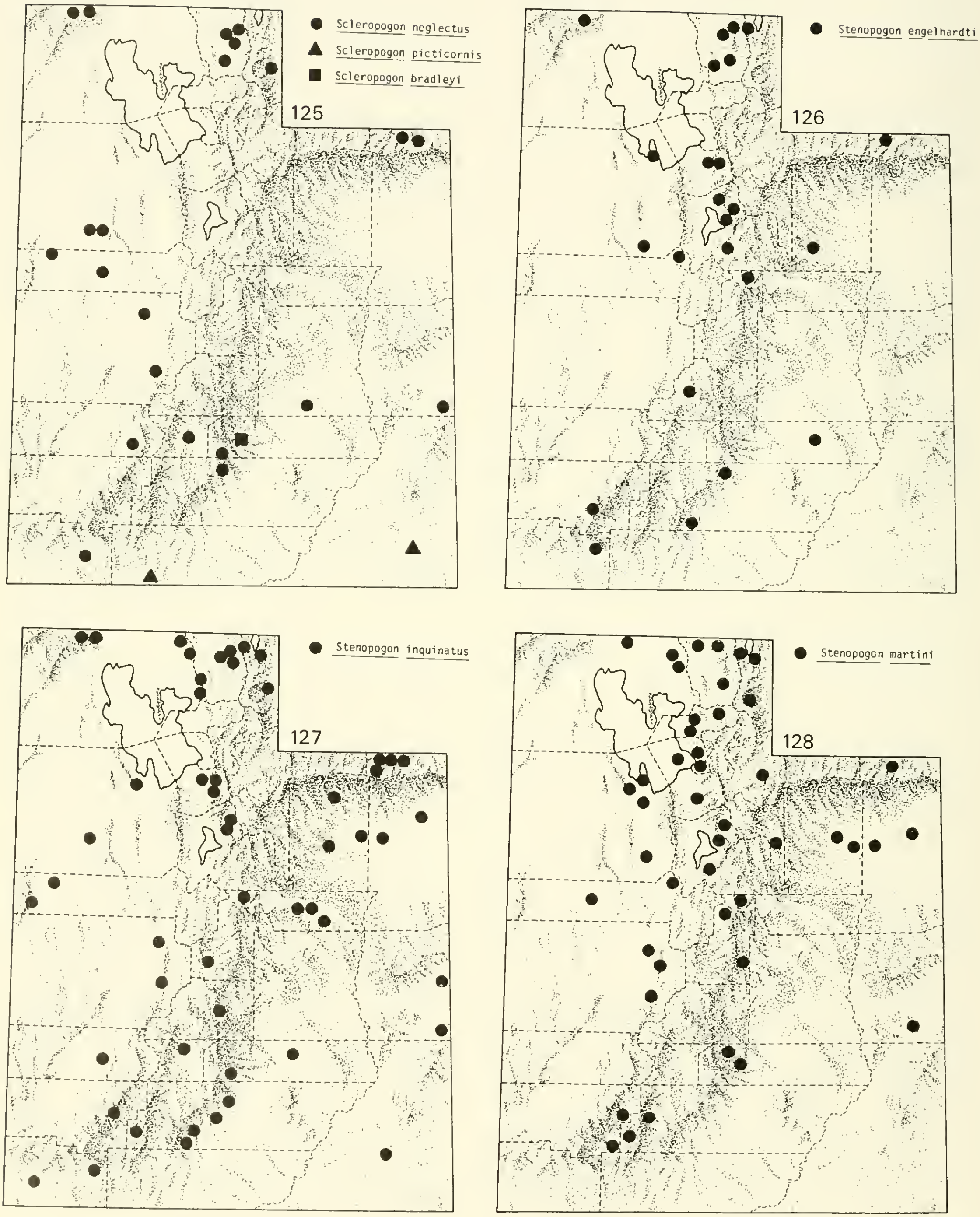
LIST OF MUSEUM ABBREVIATIONS

AESP	American Entomological Society, Philadelphia
AMNH	American Museum of Natural History
BYU	Brigham Young University
CAS	California Academy of Sciences
CEU	College of Eastern Utah
CIS	California Insect Survey
CNC	Canadian National Collection


● Scleropogon neglectus
▲ Scleropogon picticornis
■ Scleropogon bradleyi
125
● Stenopogon engelhardti
126
● Stenopogon inquinatus
127
● Stenopogon martini
128

Figs. 125–128. Utah Asilidae, distribution: 125, *Scleropogon neglectus*, *Scleropogon picticornis*, and *Scleropogon bradleyi*; 126, *Stenopogon engelhardti*; 127, *Stenopogon inquinatus*; 128, *Stenopogon martini*.

CSU	Colorado State University
KU	University of Kansas
MCZ	Museum of Comparative Zoology
OSU	Ohio State University
SUSC	Southern Utah State College
UM	University of Massachusetts
USNM	United States National Museum
USU	Utah State University
UU	University of Utah

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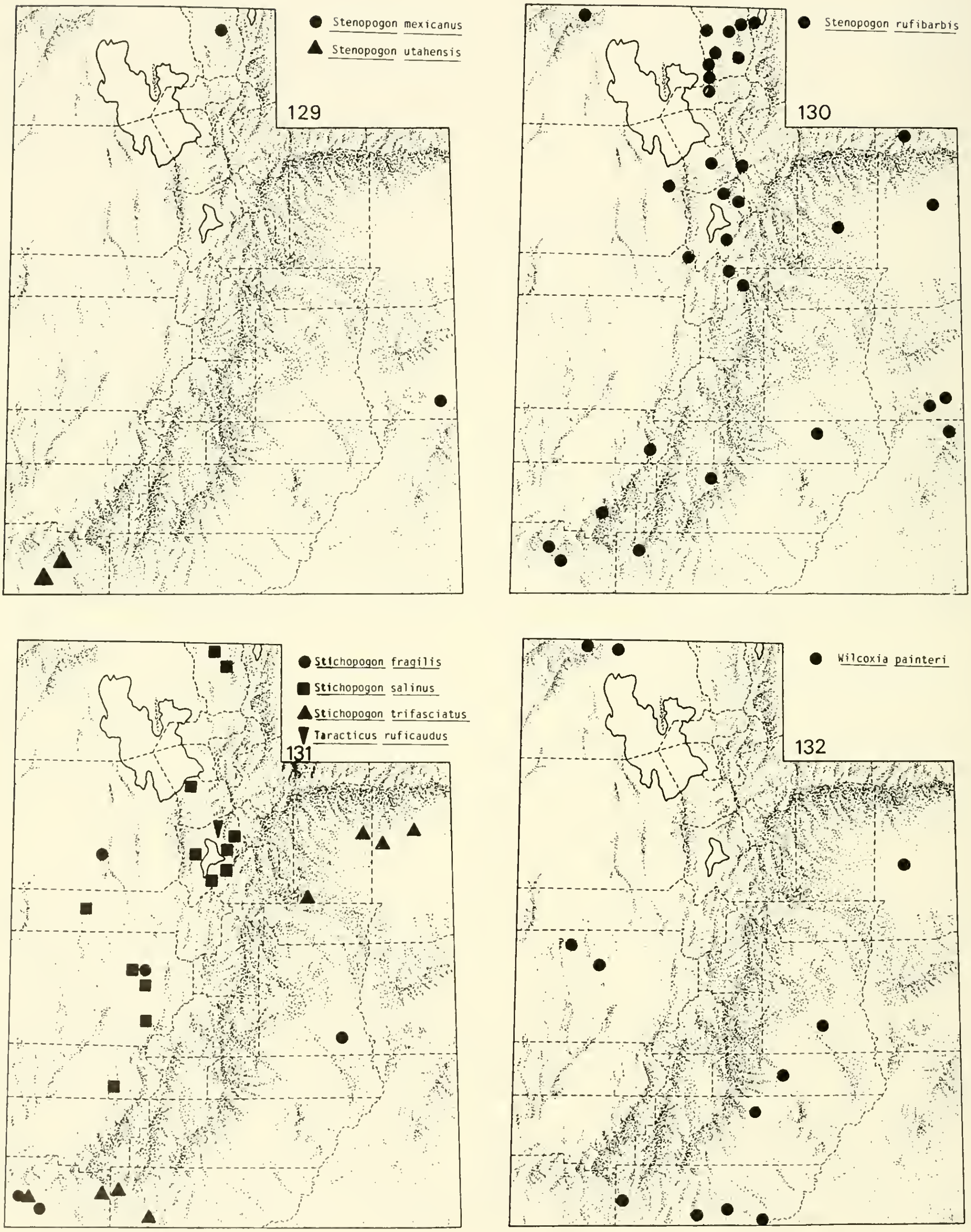
● Stenopogon mexicanus
▲ Stenopogon utahensis
129
● Stenopogon rufibarbis
130
● Stichopogon fragilis
■ Stichopogon salinus
▲ Stichopogon trifasciatus
▼ Taracticus ruficaudus
131
● Wilcoxia painteri
132
?

Figs. 129–132. Utah Asilidae, distribution: 129, *Stenopogon mexicanus* and *Stenopogon utahensis*; 130, *Stenopogon rufibarbis*; 131, *Stichopogon fragilis*, *Stichopogon salinus*, *Stichopogon trifasciatus*, and *Taracticus ruficaudus*; 132, *Wilcoxia painteri*.

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ELEMENTAL COMPARTMENTALIZATION IN SEEDS OF *ATRIPLEX TRIANGULARIS* AND *ATRIPLEX CONFERTIFOLIA*

M. A. Khan[1], D. J. Weber[2], and W. M. Hess[2]

ABSTRACT.—Seeds of two halophytes, *Atriplex triangularis*, which grows in a mesic saline marsh environment, and *Atriplex confertifolia*, which grows in a xeric desert environment, were analyzed by energy-dispersive X-ray microanalysis for the distribution of elements. The highest concentration of sodium, chlorine, potassium, and calcium was present in seed coats of *A. triangularis*. All of the elements detected were at low concentrations in the endosperm. Embryos contained the highest amount of phosphorus that is probably associated with organophosphate compounds. Potassium was also high in embryos. The total amount of elements in all regions of *A. confertifolia* was low as compared to *A. triangularis*. In a similar pattern sodium, chlorine, potassium, and calcium were the highest in seed coats of *A. confertifolia*. Elemental concentration was also low in the endosperm. Likewise, the phosphorus level was the highest in the embryo. The results support the concept of elemental compartmentalization in seeds of these halophytes.

Halophytes are plants that grow and complete their life cycles in habitats of high salinity. Although *Atriplex* spp. do not require other than trace amounts of Na^+ for normal growth, they frequently grow better in the presence of NaCl (Osmond et al. 1980). *Atriplex* spp. from different environments are characterized by high levels of NaCl in shoots, particularly in halophytes of arid shrublands (Hansen and Weber 1975, Osmond et al. 1980). However, few reports are available on the status of ions present in *Atriplex* seeds. Ungar (1984) reported that the ions of seeds of *Atriplex triangularis* constitute 2% of the total dry weight as compared to about 14% in leaves. He suggested that halophytes regulate ion distribution so that the ion concentration in seeds is low. Several studies have been done on the distribution of elements in seeds of glycophytes (Lott et al. 1982, Tanaka et al. 1977, Hofsten 1973). However, little information is available on the ion compartmentalization within different parts of seeds of halophytes. Other plant parts of glycophytes have been studied using energy-dispersive X-ray microanalyses (Bennett and Wynn Parry 1981, Saka 1982, Strullu et al. 1981). Therefore, the purpose of this investigation was to determine the elemental distribution in the seeds of these two halophytes (*Atriplex* spp.) grown in different saline environments. A clear understanding of the type and dis-tribution of elements is needed to understand the factors involved in seed germination of halophytic plants.

MATERIALS AND METHODS

Seeds of *Atriplex triangularis* Willd. were collected from a salt marsh at Rittman, Ohio, and seeds of *Atriplex confertifolia* (Torr. and Frem) S. Wats were obtained from Howard Stutz (Brigham Young University), who collected them from the desert areas of central Utah. These seeds were sectioned with razor blades and mounted on carbon stubs with graphite glue. Energy-dispersive X-ray microanalysis (EDS) was conducted with an EDAX 9100/70 with auto-calibration for automated analysis. The background was subtracted automatically. The X-ray analysis system was interfaced with an AMRay, 1000 A SEM. The seeds were not coated since the coating interferes with EDS analyses. The accelerating voltage for analysis was 20 Kv, the beam current was 75 uA, and analysis times were 100 sec at about 3,000 cps. The take-off angle was 45° with respect to the cut surface. Four different seeds for each species were analyzed in three different regions. Each region of each seed was analyzed four times at four different locations to provide a statistical basis for determining variability. Oneway ANOVA and Fischer's LSD multiple comparison tests were used for statistical analyses.

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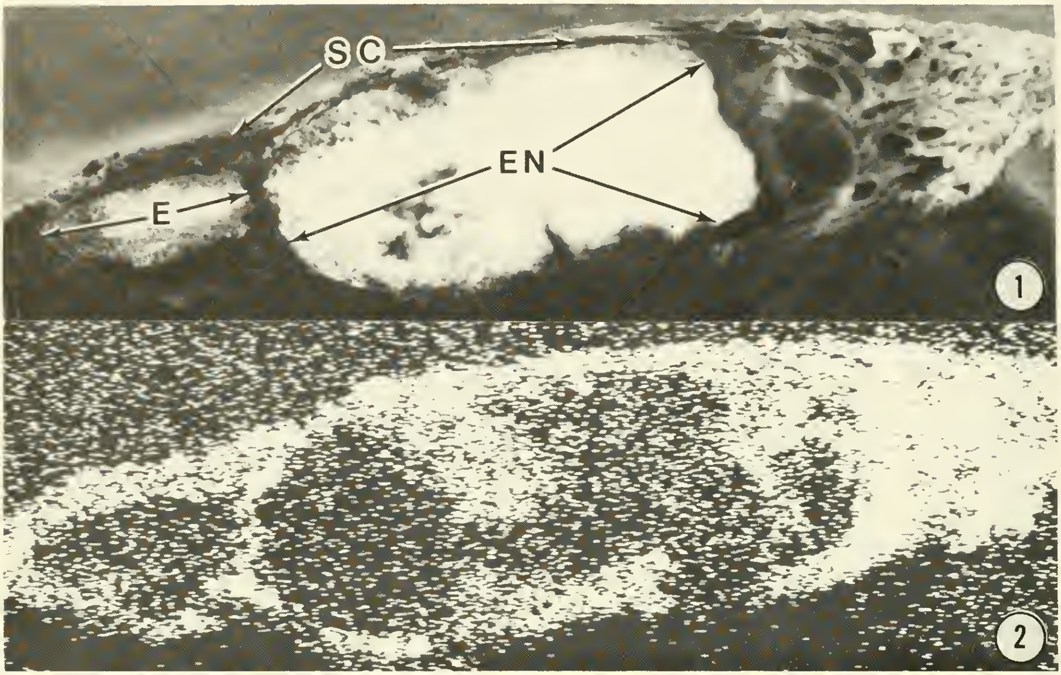

Figs. 1–2. *Atriplex triangularis:* 1, Scanning electron micrograph of a cross section of an uncoated seed showing the embryo (E), endosperm (EN), and seed coat (SC), 120X; 2, Scanning image of X-ray signals for chlorine (white image) of the same cross section of the seed shown in Fig. 1, 120X.

Results

Results obtained with both species of *Atriplex* are shown in Figures 1–4. Higher concentrations of some elements were present in *A. triangularis* seed coats and embryos than in seed coats and embryos of *A. confertifolia*, but endosperms of seeds of both species were low in all elements. There were no significant differences in elemental content of the endosperm of the two species.

Sodium, chlorine, and calcium in the seed coats of *A. triangularis* were significantly higher (5% level) than in the endosperm and embryo. On the other hand, the elements that were higher (5% level) in the embryo than in the seed coat were magnesium, aluminum, phosphorus, and sulfur. Potassium was significantly different in seed coats and embryos as compared to the endosperm.

A. confertifolia seeds contained more potassium and calcium in the seed coat (5% level) than in the embryo. The highest concentration of phosphorus was in the embryo (5% level), and the amount of potassium in the embryo and seed coat was significantly higher (5% level) than in the endosperm.

Discussion

The regions of the seed studied not only differed in elemental composition but also in relative concentrations. A comparison of these two halophytic plants indicates the concentrations of elements present in *A. triangularis* seeds were much higher than in *A. confertifolia* seeds, particularly chlorine and potassium. The high concentrations of potassium may be related to the large number of enzymes where potassium is a cofactor (Wyn-Jones and Pollard 1983).

Khan and Ungar (1984) reported that seeds of *A. triangularis* collected from a salt marsh at Rittman, Ohio, where soil salinity was about 3%, have sodium and chlorine concentrations in seeds ranging from 0.7 to 2% of the dry weight. The concentrations of these elements after analysis with X-ray microanalysis (Fig. 3) are much lower considering the fact that ionic content of leaves of *A. triangularis* may be 15% in plants growing in 3% salinity (Ungar 1984). Seeds of *Salicornia europaea* have 0.77% sodium as compared to 14.8% sodium in other parts of the plant (Poulin et al. 1978). Hocking (1982) reported that seeds of

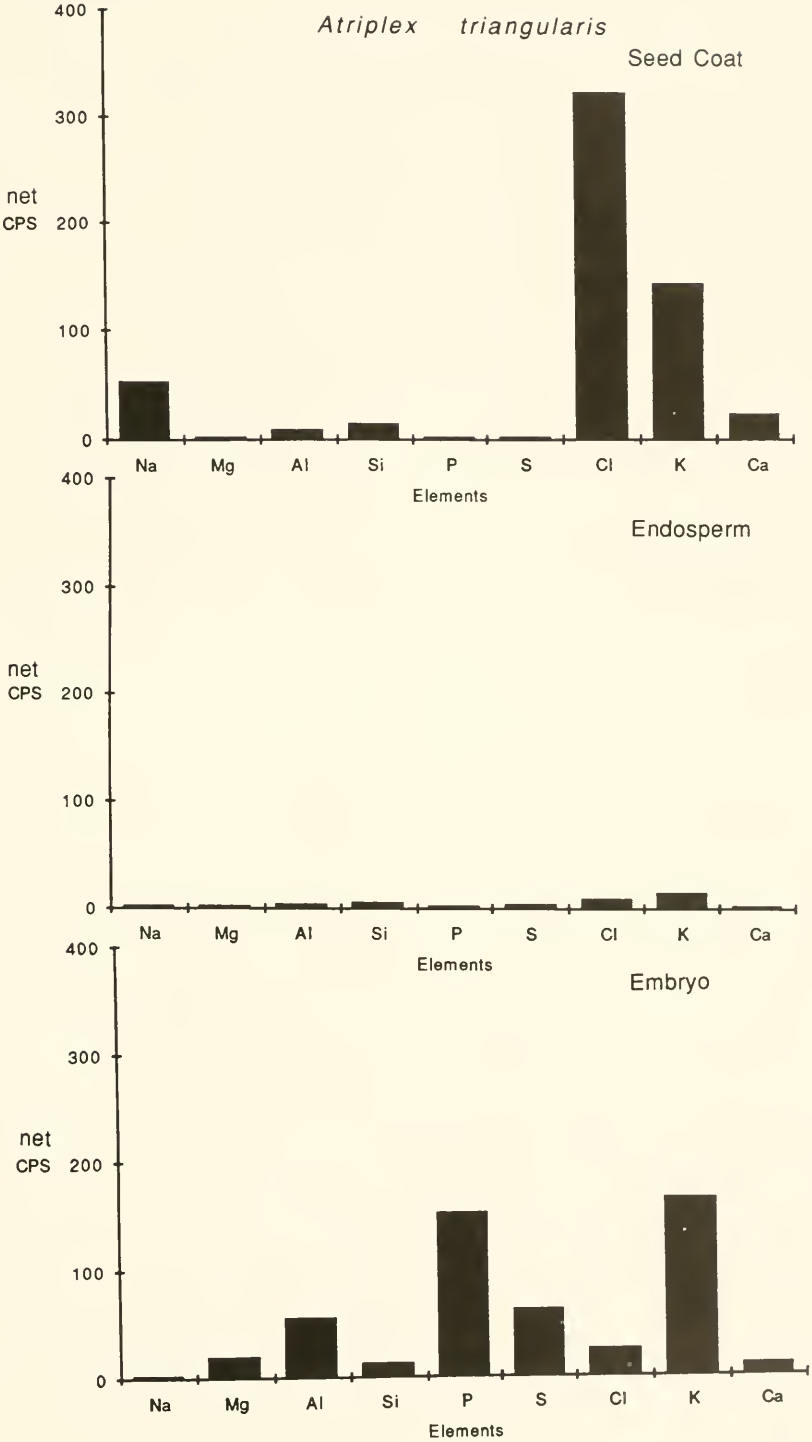

Fig. 3. Distribution of nine elements in the seed coat, endosperm, and embryo of *Atriplex triangularis* as determined by energy-dispersive X-ray microanalysis. Data is in net counts per second.

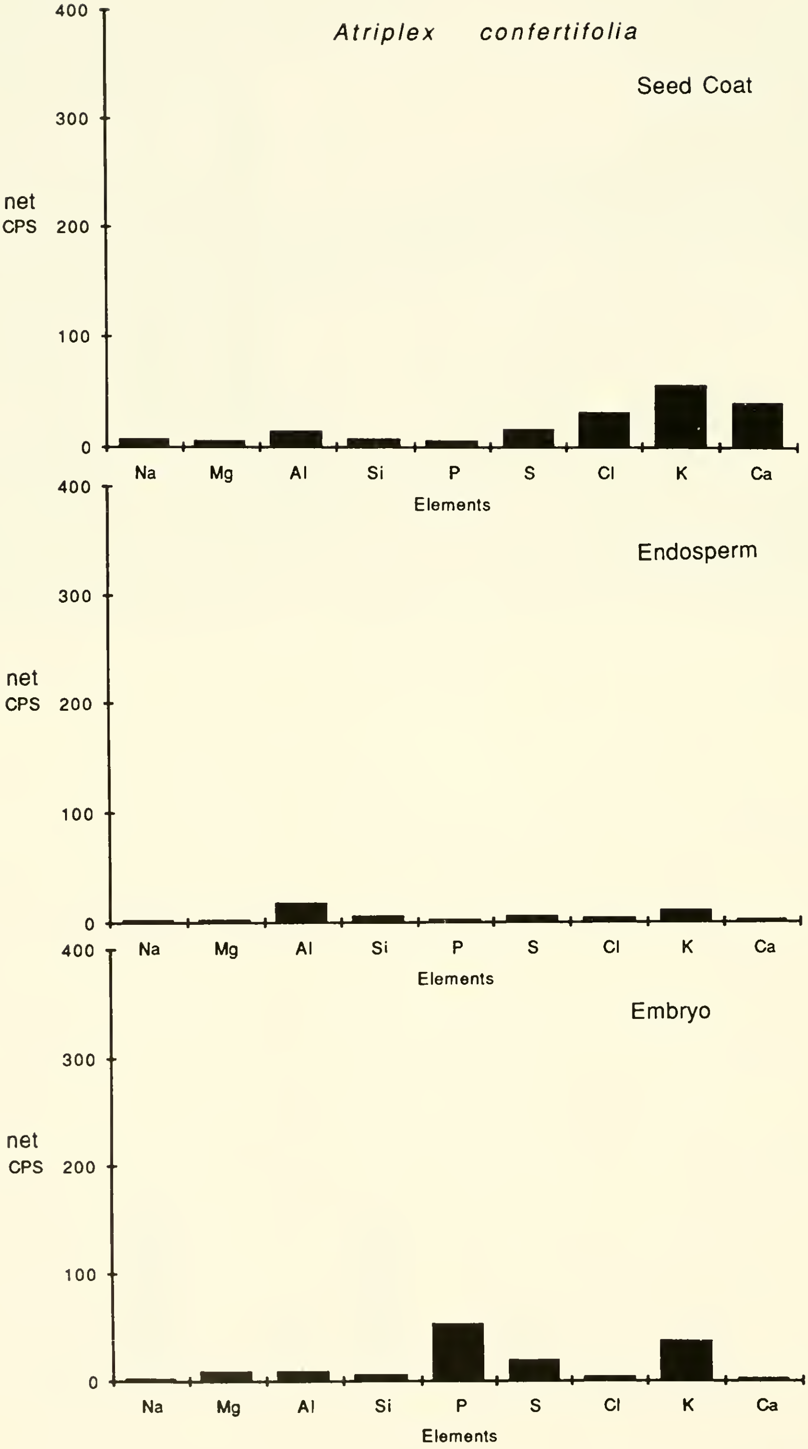

Fig. 4. Distribution of nine elements in the seed coat, endosperm, and embryo of *Atriplex confertifolia* as determined by energy-dispersive X-ray microanalysis. Data is in net counts per second.

Cakile maritima have a sodium content of 0.02% and a chlorine concentration of 0.07% compared to 14.1% chlorine and 6.8% sodium in leaves. Thus, the pattern of elemental distribution of these two species of *Atriplex* is consistent with these reports. Lott et al. (1982) observed low calcium content in the endosperm and embryo of castor bean seeds. The calcium level was also very low in the endosperm and embryo in both *Atriplex* seeds that we analyzed.

The concentration of elements in embryos was higher in *A. triangularis* seeds than in *A. confertifolia* seeds, which suggests that desert plants do not absorb or store as many elements in seeds as do salt marsh plants. These results indicate that the *Atriplex* species studied were able to compartmentalize sodium and chlorine in seed coats but reduce the levels of sodium and chlorine in embryos of their seeds. Similar results were obtained with seeds of *Salicornia pacifica* and *Atriplex canescens* by Khan, Weber, and Hess (1985).

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PLANT COMMUNITY CHANGES WITHIN A MATURE PINYON-JUNIPER WOODLAND[1]

Dennis D. Austin[2]

Abstract.—Vegetal composition was determined during 1974 and 1984 using 60 permanent 50 m^2 plots within a mature pinyon-juniper community in northeastern Utah. Results indicated that not only was there little significant change in community composition, but with many species frequency and density remained nearly the same during the decade.

Pinyon-juniper woodlands occur on over 325,000 km^2 of the intermountain region and comprise a major habitat for big game on winter ranges. However, forage productivity and variety seldom remain near optimum levels since tree density and canopy cover gradually increase with age, while understory vegetation decreases (West et al. 1979). Grazing by livestock or big game accelerates loss of understory vegetation and ground cover resulting in a further decrease of grazing capacity and increased soil erosion (Baxter 1977). Thus, a need for periodic tree control in pinyon-juniper stands is evident if maximum grazing is an objective. This paper presents data indicating little successional change of a plant community within a mature pinyon-juniper woodland during a 10-year period.

Methods

In conjunction with other studies (Austin and Urness 1976, Austin et al. 1977), 60 permanent plots were established at the foot of the Blue Mountain Anticline in the Miners Draw area of northeastern Utah in Uintah County. Plots were distributed in the zone dominated by pinyon-juniper between 1,650 and 1,850 m elevation. To insure that plots could be found in subsequent years, plot locations were preselected at specific distances and directions from evident landmarks using topographic maps and aerial photographs. Each plot was rectangular, measured 5.5 x 9.1 m, and was marked by steel reinforcement rods on all corners.

Plots were established and initial data collected during early summer 1974, with data comparably collected in 1984. In sampling, plot boundaries were defined by connecting the four corners with a string. All perennial plants within the plot were counted and recorded by species. To assure that individual plants were not missed on these large plots, a separate search was made for every perennial species, previously identified in the area, on each plot. Each plot was then searched for annual species as a group. Individual species were recorded as present, but individuals were not counted. Also recorded were maximum height and mean crown diameter, measured along the north-south and east-west axes, of juvenile (31–120 cm height) trees of pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) and shrubs of low sagebrush (*Artemisia arbuscula*), big sagebrush (*Artemisia tridentata*), and birchleaf mahogany (*Cercocarpus montanus*).

Data were analyzed using the standard and paired t-tests with a significance level of $p \leq .05$.

Results and Discussion

Few significant changes were found to occur during the 10-year period (Table 1). Only three species, needle and thread (*Stipa comata*), Fendler spring parsley (*Cymopterus fendleri*), and thickstem wild cabbage (*Caulanthus crassicaulis*), showed a significant decrease while only broom snakeweed (*Gutierrezia sarothrae*) showed a significant

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TABLE 1. Number of plants per 60 permanent 50 m^2 plots and frequency of occurrence in ( ).

TREES	1974		1984	
Juniperus osteosperma (Torr.)				
mature[1]	272	(59)	271	(59)
juvenile	44	(23)	53	(27)
seedling	39	(25)	42	(26)
Pinus edulis (Engelm.)				
mature	22	(12)	23	(12)
juvenile	13	(5)	11	(7)
seedling	53	(20)	65	(20)
SHRUBS				
Artemisia arbuscula (H. & C.)	154	(14)	185	(12)
Artemisia tridentata (Nutt.)	70	(13)	67	(13)
Atriplex canescens (Pursh)	2	(1)	1	(1)
Atriplex confertifolia (Torr. & Frem)	3	(2)	1	(1)
Cercocarpus montanus (Raf.)	8	(4)	9	(5)
Ephedra nevadensis (S. Wats.)	4	(1)	4	(1)
Ephedra viridis (Coville)	166	(22)	168	(24)
Eriogonum microthecum (Nutt.)	30	(10)	44	(10)
Forsellesia meionandra (Koehne)	2	(1)	2	(1)
Grayia spinosa (Hook.)	2	(1)	1	(1)
Gutierrezia sarothrae (Pursh.)[2,3]	302	(26)	703	(30)
Artemmisia spp. (dead skeletons)	502	(32)	435	(32)
Total (Live shrubs)[2,3]	743	(46)	1185	(51)
GRASSES-PERENNIAL				
Aristida longiseta (Stend.)	23	(3)	24	(3)
Distichlis stricta (Torr.)	42	(1)	63	(1)
Oryzopsis hymenoides (R. & S.)	14	(5)	6	(2)
Poa secunda (Presl.)	92	(23)	111	(26)
Sitanion hystrix (Nutt.)	199	(37)	301	(43)
Stipa comata (Trin. & Rupr.)[2]	4	(4)	1	(1)
Total	374	(49)	506	(50)
GRASSES-ANNUAL				
Bromus tectorum (L.)	—	(22)	—	(53)
Festuca octoflora (Walt.)	—	(4)	—	(7)
Total		(24)		(53)
FORBS-PERENNIAL				
Arenaria fendleri (A. Gray)	9	(2)	4	(1)
Aster arenosus (Blake)	1451	(24)	1502	(24)
Caulanthus crassicaulis (Torr.)[2]	62	(9)	21	(5)
Cryptantha spp.	408	(44)	692	(46)
Cymopterus fendleri (A. Gray)[2]	11	(4)	2	(1)
Echinocactus simpsonii (Engelm.)	22	(4)	34	(2)
Erigeron spp.	5	(4)	8	(2)
Eriogonum ovalifolium (Nutt.)	23	(9)	28	(9)
Erysimum asperum (D.C.)	1033	(48)	782	(53)
Gilia congesta (Hook.)	252	(32)	153	(31)
Hymenoxys richardsonii (Hook.)	37	(3)	32	(3)
Linum lewesii (Pursh)	36	(3)	21	(5)
Lithospermum ruderale (Dougl.)	8	(3)	3	(1)
Lygodesmia grandiflora (Nutt.)	3	(1)	0	(0)
Machaeranthera grindeloides (Nutt.)	91	(13)	120	(16)
Mamillaria tetrancistra (Engelm.)	1	(1)	2	(1)
Opuntia spp. (number of pads)	11679	(50)	10304	(50)
Penstemon spp.	197	(38)	367	(43)
Petradoria pumila (Nutt.)	377	(10)	347	(10)
Phlox hoodii (Richards)	4	(1)	2	(2)
Physaria chambersii (Rollins)	51	(16)	71	(14)
Senecio multilobatus (T. & G.)	46	(6)	23	(7)
Sisymbrium linifolium (Nutt.)	867	(16)	1033	(33)
Townsendia incana (Nutt.)	189	(36)	120	(32)

Table 1 continued.

FORBS-PERENNIAL continued	1974		1984	
Tragopogon dubius (Scop.)[2]	6	(3)	0	(0)
Total	16868	(60)	15671	(60)
FORBS-ANNUAL				
Camelina microcarpa (Angrz.)	—	(1)	—	(5)
Chenopodium spp.	—	(2)	—	(2)
Eriogonum cernuum (Nutt.)	—	(2)	—	(1)
Eriogonum nutans (T. & G.)	—	(3)	—	(2)
Salsola kali (L.)	—	(2)	—	(2)
Streptantella longirostris (S. Wats.)	—	(6)	—	(7)
Others	—	(13)	—	(12)
Total		(25)		(25)

[1] Defined by height: Mature = 121 + cm, Juvenile = 31–120 cm, seedling = 0–30 cm.
[2] Plant numbers significantly different between 1974 and 1984 standard t-test ($p \leq .05$).
[3] Plant numbers significantly different between 1974 and 1984 paired t-test ($p \leq .05$).

increase using the standard t-test. However, because of the small number of plants found, only the broom snakeweed was significant using the paired t-test. These data clearly showed that the plant community exhibited little change during the decade.

The number of mature trees remained the same with a combined density of 980 trees per hectare in both 1974 and 1984 (Table 1). Mean yearly height and crown diameter growth of juvenile Utah juniper were 1.8 and 1.4 cm, respectively, and for pinyon pine 1.2 and 1.0 cm, respectively.

Except for broom snakeweed, numbers of shrubs by species did not change. Dead skeletons of sagebrush (*Artemisia* spp.) were counted to possibly detect a change in density from the community prior to 1974. Although the change in dead sagebrush was also insignificant, it is interesting to note that in 1974 the ratio of dead to live sagebrush was 2.2:1.0 and 1.7:1.0 in 1984. Since numbers of live sagebrush plants showed little change, these data suggest sagebrush was more abundant prior to 1974. Mean yearly height and crown diameter growth for low sagebrush were 0.3 and 1.3 cm, respectively; big sagebrush averaged 0.6 and 1.4 cm, and birchleaf mahogany grew 3.0 and 2.3 cm, respectively. Sagebrush growth was slow but comparable to tree growth, whereas birchleaf mahogany, although found in only a few areas, did somewhat better. The total number of live shrubs showed a significant change mostly because of the increase in broom snakeweed.

Perennial grasses and forbs showed little change (Table 1). With reference to occurrence, 8 perennial species repeated the same frequency, 13 decreased, and 10 increased. The total number of perennial forbs counted did not statistically change. Excluding prickly pear (*Opuntia* spp.), 5,189 and 5,367 forbs were counted in 1974 and 1984, respectively. Even though annual grasses were found on more plots in 1984, annual forbs retained a low level of frequency.

Although this study did not show a changing trend in the understory plant community, many studies have determined an inverse relationship between density or crown cover of trees and understory production (Jameson 1967, Pieper 1977, Tausch and Tueller 1977). Since pinyon and juniper trees are more efficient competitors for soil moisture than understory vegetation, a decrease in the understory is predictable with time (West 1984). Consequently, a constant reduction of understory vegetation can be expected on disturbed sites as soon as a tree species is reestablished.

From the standpoint of big game values on winter range, these data indicate the study site carrying capacity of the mature pinyon-juniper woodland was unchanged over a 10-year period or changing at such a rate as to be statistically undetected. Even though little change in carrying capacity can therefore be predicted, it must be realized that carrying capacity was already low. Austin and Urness (1975) reported a winter deer density on the study area of about .07 deer/ha and believed the population was near carrying capacity. Treatment of the pinyon-juniper stand as previously recommended (Austin and Urness 1975) into small blocks of cleared woodland is needed if increased wildlife and livestock grazing capacities are desirable. Without treatment no change or only slow changes can be predicted in understory vegetation accompanied by increased soil erosion and loss of site productivity potential (West 1984).

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CONSUMPTION OF FRESH ALFALFA HAY BY MULE DEER AND ELK[1]

Dennis D. Austin[2] and Philip J. Urness[2]

ABSTRACT.—Tame mule deer and elk were fed fresh alfalfa hay at night and given various alternate forages during the day. This schedule, simulating farmland depredation feeding, yielded consumption values for field-growing alfalfa hay.

Depredation of standing alfalfa by big game was recognized as a problem before 1930 when deer began using summer fields in southern Utah. Use of winter haystacks in northern and central Utah was first recorded about 1930 (Low 1955). To ameliorate at least part of the problem, the Utah Division of Wildlife Resources (UDWR), formerly the Utah Fish and Game Department, began providing materials and/or building fences around highly impacted winter haystacks.

As big game populations increased, so also did the depredation problem. In 1947 the legislature passed Utah's first wildlife damage law. This legislation was designed to reduce the economic losses incurred to farmers and permitted UDWR to pay for big game depredation losses up to a maximum payment of $100 per year per landowner. More importantly, however, the law clearly indicated that the state of Utah, through UDWR, accepted at least part of the responsibility for depredation losses. The maximum payment was increased to $200 in 1953 and abruptly raised to $2,000 in 1977. An amendment considered in 1979, but which failed to pass, would have eliminated the maximum payment clause, required UDWR to pay for actual values lost, and given the total financial responsibility for depredation losses to UDWR once damage claims were filed.

Before 1977 alfalfa depredation costs paid by UDWR were minor with most years after 1956 having less than 10 claims and total payments less than $2,000. Since 1977 payments as well as fencing costs have risen dramatically with costs paid to farmers for summer field-growing alfalfa hay exceeding $29,000 in fiscal year 1984–85.

In Utah wire baskets to determine depredation loss of field-growing alfalfa hay have been utilized since 1953. To determine losses, paired plots (basketed and unprotected) were established as soon as possible following depredation complaints and hand clipped just prior to field cutting (Pederson 1982). Although the basket technique is widely used (Tebaldi and Anderson 1982), it has several difficulties. The time requirement to establish, clip, and remove plots is very great, and the consistency of clipping and removing of materials is questionable. Furthermore, the number of plots used is usually few, and data on the number of plots required for a statistically sound sample are largely unavailable. Nonetheless, Pederson (1982) recommended the use of one basket per 10 acres but added confidence intervals were wide. Palmer et al. (1982) used a density of one basket per 0.74 acres.

An alternative method of determining depredation loss is the counting of depredating animals and assuming a consumption rate. Although this method has been used successfully, a major difficulty has been estimating the amount of hay consumed, particularly when rangeland forages are also consumed. In this report, data are presented for field alfalfa consumed under varying conditions by mule deer and elk.

METHODS

Six tame adult mule deer, two bucks and four does, and four adult tame elk, one mature castrated bull and three cows, were fed alfalfa hay in summer to determine consumption. Deer and elk were kept separate, with each group collectively maintained in pens measuring about 25 x 40 m. In each trial animals were given access to fresh alfalfa hay for three consecutive nights. Hay, exceeding observed consumption, was cut and weighed each evening with orts weighed the following morning. Samples of both fresh hay and orts were collected daily for converting to dry weight consumption. A minimum of one day separated each trial.

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Three treatments were imposed and replicated three times in a random block design. In treatment 1 no other feeds were available to deer or elk. In treatment 2 lamb-grower pellets were offered to deer in excess of consumption while elk were given access to about 12 ha of dryland, grass pasture. In treatment 3, in addition to the feeds available in treatment 2, both deer and elk were given daily a variety of common browse and forb forages in excess of consumption. These forages included quaking aspen (*Populus tremuloides*), common chokecherry (*Prunus virginiana*), willow (*Salix spp.*), Saskatoon serviceberry (*Amelanchier alnifolia*), Rocky Mountain maple (*Acer glabrum*), mountain snowberry (*symphoricarpos oreophilus*), mulesear wyethia (*Wyethia amplexicaulis*), Fremont geranium (*Geranium fremontii*), and minor amounts of several other species.

In addition to the pen trials, five deer, one buck and four does, were taken to a mountain enclosure containing 2.4 ha. The enclosure described by Smith et al. (1979) was dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*) with smaller amounts of several other shrubs and a large variety of grasses and forbs in the understory. Alfalfa hay was fed as described above with no supplements during the first three consecutive trial periods. Pellets were offered in excess of consumption during the next three trials when preferred forages of low abundance had been largely consumed.

Following feeding trials, deer and elk weights were obtained. Forage and orts samples were dried at 55 C for 24 hours and weighed.

TABLE 1. Daily consumption of fresh alfalfa hay by mule deer and elk during summer 1985 (kg oven-dry hay/100 kg live animal).

A. Deer consumption in a small enclosure

	Treatments		
	1	2	3
Beginning date	None	Pellets	Browse and pellets
7-1-85	$1.22^{a(1)}$	0.91^{b}	0.87^{c}
7-13-85	$1.48^{bc(2)}$	1.15^{d}	$0.93^{(3)}$
7-25-85	1.78^{abcde}	1.57	0.97^{e}
Mean	1.49^{f}	1.21	0.92^{f}

B. Elk consumption in a small enclosure

	Treatments		
	1	2	3
Beginning date	None	Dry pasture	Browse and dry pasture
6-17-85	1.41	0.98^{ab}	0.91^{c}
7-3-85	1.43^{a}	1.06^{d}	1.11^{e}
7-15-85	1.63^{bcde}	1.39	1.15
Mean	1.49^{f}	1.14	1.06^{f}

C. Deer consumption in a mountain enclosure

Beginning date	All forages	Beginning date	Pellets and all forages
8-15-85	0.92	8-24-85	0.73^{abcd}
8-18-85	1.12^{a}	8-27-85	1.00^{c}
8-21-85	1.33^{b}	8-30-85	0.97^{d}
	1.12		0.90

(1) Figures followed by a common letter are significantly different ($P < .05$).
(2) Figure based on two days feeding.
(3) Figure based on four days feeding.

RESULTS AND DISCUSSION

In general, daily consumption of alfalfa varied according to the alternate foods available (Table 1). As expected, consumption of alfalfa hay decreased as alternate feeds were increased for both deer and elk. Thus, when no other feeds were available, alfalfa consumption was highest; it was lowest when browse plus pellets or pasture were available. Hay consumption also increased as the summer progressed. This was due to increases in metabolic rate and physical condition of animals (Moen 1978).

Consumption of alfalfa hay when based on an intake rate per unit of body weight was determined to be very similar between deer and elk (Table 1). In treatment 1, where no other feeds were available, deer and elk averaged an intake of 1.49 kg/100 kg. Since the alternate feeds in treatments 2 and 3 were not the same for deer and elk, direct comparisons are difficult to interpret. However, in treatment 3 both deer and elk had several alternate feeds available in excess of consumption, with deer averaging an alfalfa intake of 0.92 kg/100 kg and elk 1.06 kg/100 kg. The decrease of consumption in alfalfa hay from treatment 1, with no other feeds, to treatment 3, with several other feeds, was 38% for deer and 29% for elk.

The feeding trials for deer in the mountain enclosure yielded additional valuable comparisons and support of the pen data. Over the six enclosure trials with rangeland forages available deer averaged 1.01 kg/100 kg of alfalfa hay consumption compared to 0.97 kg/100 kg in the last comparable pen trial. The increase in alfalfa hay consumption over time for the first three enclosure trials was probably due to preferred forage depletion within the enclosure. As preferred forages became exhausted, alfalfa hay consumption increased. Austin et al. (1984), working on similar rangeland, showed highly preferred forages in low abundance were rapidly depleted even though other preferred forages were abundant. The small change in alfalfa consumption between the final two trials suggested preferred forages of low abundance were depleted and deer diets were static.

In other research Tevaldi and Anderson (1982) determined, using fecal materials, that alfalfa comprised only 30% of diets from deer using alfalfa fields. However, they opted to recommend using 50% dietary contribution because of additional losses to trampling and bedding, and the more complete digestion of green alfalfa hay as compared to shrubby species (Anthony and Smith 1974). Applying Alldredge et al. (1974) consumption rates, Tebaldi and Anderson (1982) produced consumption rates of 0.63 and 1.05 kg/100 kg at 30% and 50% diet contribution, respectively, the latter figure being very comparable to our data.

The data presented in Table 1 establish outside boundaries for depredation determination of field-growing alfalfa. Because rangeland situations are highly variable, animals will have access to greatly different range and forage conditions during the day when away from alfalfa fields. Consequently, we recommend evaluating the daytime rangeland used by depredating animals and adopting or interpolating a consumption value.

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HELMINTH PARASITES OF THE WYOMING GROUND SQUIRREL, *SPERMOPHILUS ELEGANS* KENNICOTT, 1863

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ABSTRACT.—Helminth parasites of the Wyoming ground squirrel, *Spermophilus elegans* Kennicott, 1863, were surveyed from two environmentally different habitats within Wyoming. A total of four helminth species were identified. Three helminth species were found in 419 hosts collected in a mesic habitat including one species of adult cestode, *Hymenolepis citelli*, and two species of nematodes, *Citellinema bifurcatum* and *Syphacia citelli*. Only larval cestodes (*Taenia taxidiensis*) were found infecting 335 Wyoming ground squirrels collected from a xeric habitat.

The helminth parasites of ground squirrels belonging to the genus *Spermophilus* have not been investigated throughout much of their range. Such studies as those of Jenkins and Grundmann (1973), Babero (1973), and McGee (1980) examined helminths from these hosts in Utah, Nevada, and Saskatchewan, respectively.

In conjunction with studies on the coccidian parasites of the Wyoming ground squirrel, *Spermophilus elegans* Kennicott, 1863, each host was also examined for the presence of helminths. Until 1984, *S. elegans* was classified as a subspecies of *S. richardsoni*; thus, this is the first report of helminths from *S. elegans*.

The ground squirrels we examined were collected from two study areas in Wyoming by snap trapping and shooting. The first area is a sprinkler-irrigated alfalfa and brome grass field (105°33′W, 41°12′N) located approximately 18 km south of Laramie, Wyoming, at an elevation of about 2,250 m with annual precipitation of 26 cm. The second study area of desert shrub-steppe (107°45′W, 41°17′N) is approximately 33 km north of Baggs, Wyoming, at an elevation of about 1,950 m with an annual precipitation of 15 cm. Approximately 240 km separate the two study sites. We hypothesized that a greater number of squirrels would be infected with helminths in the more mesic irrigated alfalfa and that different helminth species would be found in the two host populations because of differing climatic moisture conditions.

MATERIALS AND METHODS

Each ground squirrel collected from 1983 to 1985 was weighed, sexed, and individually bagged for shipment to the laboratory in Laramie where the animals were necropsied. The small intestine, caecum, and large intestine were opened in containers of tap water. After the contents of the digestive tract were stripped into their respective containers, the water was decanted, and the remaining sediment was examined for the presence of helminths using a dissecting microscope.

Recovered cestodes were relaxed in tap water containing several drops of pentabarbitol sodium, fixed in hot 10% formalin, and stained in Semichon's acetocarmine. Following staining, representative specimens were cleared in terpineol, washed in xylene, and mounted permanently in Permount. Nematodes were fixed using hot 70% ethyl alcohol, cleared in 70% ethyl alcohol + 5% glycerine, and mounted permanently in glycerine jelly. Scolices from metacestodes were mounted in Hoyer's solution. Representative specimens have been deposited in the National Parasite Collection, Agricultural Research Service, Beltsville, Maryland (USNM Helm. Coll. No.   ).

RESULTS AND DISCUSSION

From the 419 ground squirrels examined from the irrigated field, two species of nematodes and one species of cestode were found. From the 335 squirrels collected from the shrub-steppe, no adult helminths were

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TABLE 1. The occurrence of helminths in two populations of the Wyoming ground squirrel.

	Number of hosts positive	
	Mesic (irrigated) n = 419	Xeric (desert) n = 335
CESTODES		
Hymenolepis citelli	3 (0.7%)	0
Taenia taxidiensis	0	3 (0.9%)
NEMATODES		
Citellinema bifurcatum	88 (21.0%)	0
Csyphacia citelli	77 (18.4%)	0

found, and only one species of metacestode was present (Table 1).

Cestodes

***Hymenolepis citelli* McLeod**, 1933 (U.S. Helminthol. Coll. No. 79052). Cestodes of this species were found in 3 of 419 (0.7%) squirrels collected in the irrigated study site. This low incidence of infection is considerably below those reported from Utah in *S. variegatus* (3%), *S. lateralis* (2%), and *Ammospermophilus leucurus* (6%) (Jenkins and Grundmann 1973). McGee (1980) found 6 of 209 *S. richardsoni* (3%), 8 of 31 *S. tridecemlineatus* (26%), and 7 of 46 *S. franklini* (15%) infected with this cestode. No hosts from the desert study area were infected with this helminth. It is possible that the irrigated field provided a more suitable environment for the invertebrate intermediate host of this cestode.

***Taenia taxidiensis* Skinker**, 1935 (U.S. Helminthol. Coll. No. 79051). Metacestodes of this species were found in 3 hosts from the desert study site (0.9%). Jenkins and Grundmann (1973) and McGee (1980) reported 2% of 154 *S. variegatus* and 2% of 46 *S. franklini* to be infected with this metacestode in Utah and Saskatchewan, respectively. No metacestodes of this species were found in hosts collected in the irrigated study area although badgers, *Taxidea taxus*, the definitive host for this helminth, were frequently encountered on the study area and were known to harbor adults of this species.

Nematodes

***Citellinema bifurcatum* Hall**, 1916 (U.S. Helminthol. Coll. No. 79050). Nematodes of this species were found in the small intestine of 88 of 419 (21%) hosts collected in the irrigated study area. No individuals from the desert were infected. This level of infection is comparable to values reported by Jenkins and Grundmann (1973) and McGee (1980). This nematode appears to be a widespread helminth as it has been reported from six species of *Spermophilus* as well as *Tamiasciurus hudsonicus* by the above two authors.

***Syphacia citelli* Tiner & Rausch**, 1950 (U.S. Helminthol. Coll. No. 79049). This caecal nematode was found in 77 of 419 squirrels (18%) collected in the irrigated habitat. As with the previous species, no squirrels were found to be infected with *S. citelli* in the desert. This species was found in 2 of 209 *S. richardsoni* (1%) examined by McGee in Saskatchewan but was found in large numbers of *S. variegatus*, *S. armatus*, and *S. beldingi* (66%, 63%, 8% respectively) in Utah (Jenkins and Grundmann 1973).

CONCLUSIONS

The presence of both adult cestodes and nematodes in the irrigated habitat and the absence of the same species from hosts collected in the more xeric habitat indicate that moisture may be a factor in furthering the life cycle of helminths of ground squirrels as it is for other helminths (Soulsby 1977). However, Jenkins and Grundmann (1973) found various species of ground squirrels from arid or xeric habitats infected with the same species of helminths that we found only in the mesic habitat.

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OBSERVATIONS OF CAPTIVE ROCKY MOUNTAIN MULE DEER BEHAVIOR

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ABSTRACT.—Observations were made on the behavior of a captive herd of Rocky Mountain mule deer (*Odocoileus hemionus hemionus*). Comparisons in general behavior patterns were made between captive and wild deer. Similar behavior was exhibited by captive and wild deer. Captive deer (as well as other species) may be useful for study of certain behavioral aspects of their wild counterparts.

Literature discussing general behavioral observations of captive deer (*Odocoileus* spp.) is limited (Browman and Hudson 1957). The effects of captivity on many facets of deer behavior are unknown, particularly for deer that are born and raised in captivity. This note summarizes five years of observations on the behavior of tame, captive Rocky Mountain mule deer (*O. hemionus hemionus*) and compares this to behavioral observations reported for wild deer. We suggest that observations of captive mule deer can be used to predict wild deer behavior.

METHODS

Incidental observations were made while conducting other research at an enclosure located 3.2 km west of Fort Collins, Colorado, where deer have been raised for radioecological studies since the early 1960s. The 0.3-ha enclosure was subdivided into four 0.08-ha sections. The northwest subdivision was further divided into several isolation pens. Alfalfa, stock pellets, garden fruits and vegetables, and water were provided in each subdivision *ad libitum*. Deer also grazed upon various forbs and grasses, particularly blue grama (*Bouteloua gracilis*), growing in the enclosures.

Observations were made from August 1972 through August 1977. All tame mule deer in this colony were hand-fed from birth to facilitate easier handling during research studies. There were 12 adult, 5 male and 7 female, and 13 fawns, 5 male and 8 female, held for observation (Halford and Alldredge 1978). As a safety precaution, antlers were removed as soon as they ceased growing, usually in late August. With the exception of the observers (three during this study), the deer had minimal human contact. Most observations were made from distances of 10 to 30 m by observers who tried to remain inconspicuous. Feeding and bedding, aggressive behavior, fawning and breeding, as well as deer interactions, were observed.

RESULTS AND DISCUSSION

Captive deer showed preference for succulent materials such as grapes, apples, and lettuce. Feeding deer were observed to select red and yellow fruits and vegetables before green fruits and vegetables. The deer fed in an unhurried and relaxed manner, frequently looking up or moving away from the food. Dorrance (1965) observed that wild mule deer fed slowly and appeared to eat the most succulent items first.

After eating, captive deer often bedded down. Dominant deer would occasionally force a bedded deer out of its bed and select that bed. When selecting a bed, a deer approached an area, smelled it, and then lay down in one of several positions. Ordinarily, a deer rested with the forelegs flexed under the chest, with head up and slightly to one side, and with one hind leg exposed along the same side (Linsdale and Tomich 1953, Geist 1981). Deer also extended one foreleg forward or lay the head back upon their side. We occasion-

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ally observed deer resting with eyes closed. Captive deer performed comfort movements described by Geist (1981) when the resting period was over.

Aggressive behavior was most frequently observed during feeding. The one-footed kick was used most frequently in a feeding conflict (Dorrance 1965, Geist 1981). This behavior occurred frequently in the captive deer herd. The dominant animal (usually a large buck or doe) would walk behind a subordinate that was attempting to feed and strike it with a front foot without rearing. Similar behavior was observed in wild deer (Bailey 1960). Aggressiveness was also observed in fawns. For about three months post-partum, individuals would be aggressive toward the handler (lunge at bottle and handler) during feeding but not toward other fawns. This aggressiveness was likely a result of hunger. However, a definite "peck" order appeared to develop after about three months, with the larger (and usually older) fawns being more dominant. Older fawns were removed when unweaned fawns were being fed to prevent aggressive kicking. This kicking was not as frequently observed in fawns as it was in adults.

Captive bucks began to show aggressive behavior after velvet stripping. Velvet stripping by captive deer began in September with the youngest bucks stripping first. Bucks stripped velvet by rubbing antlers on rocks, fence posts, feed and water containers, buildings, and vegetation. When removing velvet on vegetation, a buck would place his antlers in a patch of weeds and shake his head vigorously. We also observed an adult buck chewing on the velvet of a yearling buck. Antler rubbing may provide practice for later contests between bucks (Linsdale and Tomich 1953).

When bucks had antlers, the largest buck became the dominant animal. During feeding, other deer would leave the feeding bin and observe from 15 to 20 m as the dominant buck approached and fed. If a subordinate animal did not yield to the dominant buck, he would often butt the subordinate with his antlers. Bailey (1960) observed that dominant animals (does or bucks) had first choice of food. He also reported that the claiming of a feeding spot was usually done without raising the hairs along the neck and laying the ears back (aggressive posture). Captive deer frequently showed aggressive behavior (kick or butt) at the feeding station as they crowded around the small area. We observed no aggressive behavior when captive deer fed on vegetation in the enclosure.

After antler drop, a large doe frequently became the dominant animal, even over bucks. Dominance was usually observed during feeding with the dominant animal chasing other deer away from the feeding area. Often the one-footed kick was used to drive away persistent deer. The dominant animal would often lower the head and advance toward the subordinate animal. This behavior was also reported in wild mule deer (Linsdale and Tomich 1953, Geist 1981). Bucks appeared to be conscious of their antlers' sensitivity and avoided any confrontations with does and bucks until the antlers hardened (late August). Confrontation between bucks was observed nearly every day after velvet was stripped. Captive bucks placed their antlers together and pushed each other back and forth, each giving way to the other. This activity usually ended after three to four minutes and was followed by feeding. However, Geist (1981) observed that sparring in wild mule deer may occasionally last more than an hour. Dorrance (1965) noted that sparring was not carried out with great vigor in wild mule deer and was engaged in for mutual enjoyment and stimulation of rutting or reproductive behavior.

Vigorous sparring usually occurred during October and November in captive deer, even those with antlers cut off. Captive bucks in our study showed the distinct components of aggression that Cowan and Geist (1961) and Geist (1981) described for wild deer and captive deer. Intensity of aggressive behavior appeared to be directly related to the age of captive deer, the older deer showing the most pronounced aggressive displays (Cowan and Geist 1961, Geist 1981). Usually the dominant deer (and oldest), or the deer initiating aggression, slowly approached the intruder with head lowered so that the neck was parallel to and on the same level as the top of the back; the muzzle was extended, the ears were laid along the neck, and the hair along the shoulders and neck was held erect, making the deer appear larger. The preorbital glands were opened in some confrontations, and a loud hissing sound was often emitted from the nostrils (Cowan and Geist 1961, Geist 1981). If the intruder or subordinate animal was not driven away by this display, the dominant animal would lunge with head lowered and drive the subordinate animal away. If both bucks showed aggressive display, the display would continue for two or three minutes with each deer apparently trying to intimidate the other. If neither deer submitted, they would suddenly lunge at one another. The bouts were very vigorous and lasted until one deer was driven away, usually within three to four minutes. There were usually no bodily injuries during these confrontations. However, in two instances, large dominant bucks with antlers sawed off were able to kill younger bucks that still had antlers. These confrontations were not observed, but autopsies of the killed animals showed extensive internal injuries. Bucks were also aggressive toward does and often butted them for no apparent reason during the rut. Einarsen (1969) found that wild bucks show a domineering nature during the breeding season, but older does are dominant during other periods.

During September and October captive bucks were observed approaching does and attempting to mount them. None of the does were receptive during our observations. Before attempting to mount a doe, a buck would approach the doe from behind as she urinated. The buck would sniff the urine and then curl the upper lip back, holding the head on a level plane with the back and waving the head from side to side (flehman). Similar behavior has been described in wild mule deer (Dorrance 1965, Geist 1981). Bucks would also place their hind legs together, urinate on the tarsal glands, and rub the glands together. Bucks urinate on their tarsal glands and rub them together at all seasons, but this habit increases during the rut (Browman and Hudson 1957). Linsdale and Tomich (1953) reported that urinating on the tarsals constituted a type of threat during the rut that is not conveyed at other seasons.

Actual copulation was not observed. Most mating occurs at night (Einarsen 1969); thus, observations of this behavior are difficult to obtain. However, all captive deer were observed mounting one another as many as three times in an hour. Adult deer of like and opposite sexes, as well as fawns, mounted one another during all seasons of the year; however, copulation was never observed. Geist (1981) noted that this behavior also occurs in wild populations but is not commonly observed. Perhaps the close association of the captive deer resulted in a higher frequency of “false mountings” than would occur in wild populations.

Parturient behavior of captive mule deer has been described previously (Halford and Alldredge 1975). Much of the parturient behavior we observed in captive mule deer was similar to that reported for wild white-tailed deer (*O. virginianus*) and black-tailed deer (*O. h. columbianus*) (Haugen and Davenport 1950, Michael 1964, Miller 1965). Several authors (Lindzey 1943, Linsdale and Tomich 1953, Dasmann and Taber 1956, Einarsen 1969) have observed pregnant does seeking thick cover for fawning. As there was little cover in the enclosures, does about to give birth usually were observed selecting sites of shelter along fences, near buildings, or under one of three roofed wind shelters in the pens.

Fawns were removed from the doe immediately after birth, placed in separate pens, and hand-fed to instill tameness (Halford and Alldredge 1978). Does bleated and paced about the pens for about three days after fawn removal. Separated fawns often mewed, and this seemed to distress the does. On several occasions when fawns were handled, they made a loud bleating noise. Immediate response from does usually occurred; the doe would run along the fence, occasionally stopping to look in the direction from which the bleat had come. Similar observations were made on wild deer by Arthur et al. (1978) wherein does became alert and curious upon hearing a fawn distress call.

During the first week after fawns were removed from the does, fawns exhibited an escape behavior similar to that reported by Dorrance (1966). When approached by humans, fawns dropped to the ground, crouched with necks outstretched, and remained motionless. Fawns would not attempt to flee until they were disturbed by the observer. This behavior pattern subsided after about a week, and fawns would then come to the researcher during feeding periods. Captive fawns would raise their tails in a vertical position prior to feeding. The tails were lowered from this position as the fawns became sated. This behavior has also been observed in wild fawns during feeding (Linsdale and Tomich 1953).

Fawns were often observed kicking one another lightly and then bucking or running. This behavior appeared to be "play." Dasmann and Taber (1956) and Linsdale and Tomich (1953) have observed wild deer at play and suggested that it may serve as a means for fawns to receive vigorous exercise. Play may also provide a way to gain information by which the fawn is "programmed" to function as an adult (Geist 1981). Fawns also were observed participating in mutual grooming, licking one another. The perianal region of one fawn was occasionally licked by another fawn, and this stimulated defecation. We have observed captive does licking the perianal region of their fawns, and this appeared to stimulate nursing and defecation (Halford and Alldredge 1978). Captive does were also observed eating the feces of their fawns during this grooming. Wild fawns have been observed nursing with their tails to the doe's head, but no mention was made of does licking the perianal region (Linsdale and Tomich 1953).

We observed the reactions of captive deer to a newly introduced tame deer. A three-month-old doe was placed in the enclosure in late August with adult deer. Bucks immediately tried to mount her, but she ran from them, continually giving a high-pitched cry. The does chased the new fawn and kicked her with their forelegs. The following day similar interactions between the does and fawn were observed; however, the bucks showed no aggression toward the fawn. On the third day the does did not actively chase the fawn, but they kicked the fawn when she approached within 0.5 m. The fawn appeared to be accepted by all deer on the fourth day. The adults no longer showed aggression toward the fawn, although she was the last to feed. Bailey (1960) observed that fawns were always subordinate in a wild herd.

Hand-raised fawns were taken to the field as part of a food-habits study (Arthur 1977), and interactions between four tame deer and wild deer were observed. The four tame deer, two yearling does and two yearling bucks, castrated as fawns, were permitted to roam freely. In most of the observations, wild deer were aware of human presence. Wild deer would often observe the tame deer from 50 to 250 m but approached infrequently. When wild deer approached the tame deer, the wild deer would assume an aggressive posture (both does and bucks) and chase the tame deer. The tame deer were often kicked by wild deer. Wild deer would chase tame deer for about 20 m. Often the tame deer would seek refuge with the observers. In none of these encounters did a tame deer dominate a wild deer regardless of the status of the tame animal within its own group.

CONCLUSIONS

Although incidental, our observations of behavior in captive deer were consistent with observations made on wild populations (Dorrance 1966, Geist 1981). Dominance and parturition behavior in captive deer were similar to that observed in wild deer (Michael 1964, Dorrance 1966, Geist 1981).

Conditions imposed by the close association of tame deer in an enclosure probably altered or intensified some behavior, particularly aggressive behavior. However, some behavioral aspects, such as parturition behavior, are very difficult to obtain in a wild deer population. Also, the mobility and wariness of wild deer make behavioral observations difficult. We also were able to observe fawn behavior in our captive deer, which would be difficult to observe in wild animals.

Therefore, close study of captive deer and perhaps other captive animals to learn about the behavior of their wild counterparts should provide useful insights into animal behavior that may otherwise be difficult or impossible to obtain.

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EFFECTS OF OSMOTIC POTENTIAL, POTASSIUM CHLORIDE, AND SODIUM CHLORIDE ON GERMINATION OF GREASEWOOD (*SARCOBATUS VERMICULATUS*)[1]

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ABSTRACT.—Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) (Chenopodiaceae) typically grows on salt-affected soils where its germination requirements may reflect characteristics necessary for establishment in saline environments. The objective of this study was to determine the effect of osmotic potential and specific ions on the germination of seeds from three populations of greasewood. Seeds were germinated at 20 C in solutions of polyethylene glycol with water potentials ranging from −0.3 to −2.2 MPa that contained 0 to 68480 μmol·L^{-1} sodium chloride (NaCl) or 0 to 53640 μmol·L^{-1} potassium chloride (KCl). Germination of two populations was reduced by increasing salt concentration and decreasing osmotic potential; germination of one population was reduced by declining osmotic potential. No seeds germinated at an osmotic potential lower than −1.6 MPa. For all populations, days to 50% of final germination increased and abnormal germination decreased as osmotic potential declined. Comparison of our results with those from other studies suggests geographic ecotypic development in response to osmotic potential and NaCl and KCl concentrations during germination.

Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) grows in all states west of the 100th meridian, northern Mexico, and southern Alberta and Saskatchewan (Branson et al. 1967). Throughout its range, greasewood usually grows on fine-textured soils that are saline or alkaline, but occasionally it grows on nonsaline and coarse-textured soils (Shantz and Piemeisel 1940, Fireman and Hayward 1952, Gates et al. 1956, Rickard and Keough 1968). Because greasewood grows on a variety of soils, we hypothesized that populations from different sites would respond differently to osmotic potential and specific ions during germination.

Seed germination and seedling establishment may be the most critical stages in life cycles of plants in saline environments. The soil conditions to which seeds and seedlings will be exposed determine their success (Ungar 1982) and are a major source of attrition in the seedbank (Harper 1977). Salinity may affect germination and seedling growth through reduced osmotic potential, increased availability of a toxic ion, and reduced absorption of nutrients because of ion imbalance (Richards 1954, Hayward and Bernstein 1958). Generally germination is delayed and reduced when salt stress exceeds a critical level; the level of salinity at which germination is reduced varies with species, genotype, environmental conditions, osmotic potential, and specific ions (Ungar 1978).

Chapman (1974) concluded that a reduction in soil salinity is requisite for germination in saline environments. Reduction of soil salinity increases the osmotic potential and reduces ion concentrations (Richards 1954). Germination of some species is reduced more by osmotic potential than by specific ions (Choudhuri 1968, Ungar and Capilupo 1969, Ungar and Hogan 1970, Macke and Ungar 1971, Cluff et al. 1982); however, ions depress germination more than osmotic potential in other species (Choudhuri 1968, Hyder and Yasmin 1972, Redmann 1974, Wood et al. 1976, Young and Evans 1981). The effects of osmotic potential and ions also vary within species (Dewey 1960, Springfield 1966, Workman and West 1967, Clarke and West 1969, Clarke and West 1972), and differences may be related to genetics or environmental conditions.

The objective of this research was to ascertain the effects of osmotic potential and ions on the germination of greasewood. Seeds of three greasewood populations were incubated in a gradient of osmotic potentials and concentrations of KCl and NaCl.

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MATERIALS AND METHODS

Three sources of greasewood seeds were collected from sites located approximately 30 km south of Burns, Oregon. Elevation of all sites is approximately 1,255 m, and climatic conditions are similar. Soils of the North and South Harney sites were formed from alluvial materials and are moderately well drained, fine-loamy, mixed, mesic Xerollic Haplargids and fine-loamy, mixed, mesic Xerollic Camborthids, respectively. Soils at the Coyote Buttes site are moderately well drained, fine montmorillonitic, mesic Xerollic Haplargids, formed from alluvial materials.

Seeds (utricles) were collected from several plants at each site in October 1982. After collection, seeds were dried at room temperature and stored in paper envelopes. Bracts were removed with a flail, and seeds were sorted with air to reduce variation in size; the heavier one-half of each seedlot was used for germination trials. Seeds were approximately eight months old when tested.

Five osmotic solutions were prepared by adding polyethylene glycol (M.W. 20000) to distilled water. Solutions were buffered to pH 8.0 with (Tris-[Hydroxylmethyl] Amino-Methane) buffer. Each solution was divided into 9 aliquots, and 2 M sodium chloride (NaCl) or potassium chloride (KCl) was added to bring solutions to 0, 8560, 17120, 34240, and 68480 $\mu mol \cdot L^{-1}$ for NaCl and 0, 6705, 13410, 26820, and 53640 $\mu mol \cdot L^{-1}$ for KCl. Salt concentrations were selected to bracket K^+ and Na^+ concentrations determined for saturation extracts (Richards 1954) from soils collected from the top 5 cm of the solum in four greasewood communities. Sodium and potassium concentrations ranged from 27000 to 75000 and 11278 to 26739 $\mu mol \cdot L^{-1}$ of saturation extract, respectively. Concentrations ranged from 2750 to 5500 $\mu mol \cdot L^{-1}$ for calcium and 1200 to 3250 $\mu mol \cdot L^{-1}$ for magnesium.

Osmotic potentials of germination solutions, determined on the fourth and eighth days of incubation, were −0.3, −0.7, −1.2, −1.6, and −2.2 MPa for both NaCl-PEG and KCl-PEG solutions. Although the addition of NaCl and KCl may have reduced osmotic potentials, no differences were found between the various concentrations. Osmotic potentials were determined from filter paper discs, 5 mm in diameter, placed in petri dishes when incubation was initiated. Osmotic potentials of these discs were determined with a Wescor[4] HR-33T microvoltometer and a Wescor[4] C-52 sample chamber psychrometer after calibration with standard NaCl solutions.

Before commencing germination tests, lots of 50 seeds were counted and stored in paper envelopes. Ten envelopes of each collection were randomly selected and used for determining seed weights. Another set of envelopes was randomly selected, and seeds were placed in petri dishes on a #4 Whatman[4] filter paper disc that was underlaid by germination blotter. Twenty-five ml of osmoticum were added to each dish, and the dishes were covered and sealed in plastic bags to prevent desiccation. Seeds were incubated in darkness at 20 C for 14 days and exposed to light only briefly when germination was recorded at two-day intervals. Seeds were considered germinated when the embryo had uncoiled and cotyledons were reflexed. Seeds that initiated germination but failed to meet the germination criteria were recorded as abnormal germination. At the end of the incubation period, ungerminated seeds were dissected to determine seed fill. The number of days to 50% of final germination was used as a measure of germination rate.

Within salts, treatments were applied factorially in a randomized complete block design with four replications. Factors were salt concentrations and osmotic potential. Time was used as blocks because replications were started at approximately two-week intervals.

Data were initially analyzed within seed sources with a factorial analysis of variance after transforming counts with arc sin $\sqrt{\hat{p}}$ (Snedecor and Cochran 1980). Polynomial response curves or multiple linear regression response surfaces were then developed using untransformed data (Neter and Wasserman 1974). Tukey's W-procedure was used for testing differences between means (Snedecor and Cochran 1980). All statistical tests were conducted at $p = 0.05$ probability level.

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[4] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by U. S. Department of Agriculture or Oregon State University and does not imply approval to the exclusion of other products that may also be suitable.

TABLE 1. Seed weights and seed fill for three seed collections of greasewood from southeastern Oregon.

	Collection source		
	North Harney	South Harney	Coyote Buttes
Mean weight (mg/50 seeds)	79.6[1]	97.5[1]	81.3[1]
Mean percent seed fill	96.4[2]	96.6[2]	96.0[2]

[1] HSD 12.6
[2] $S_{\bar{x}}$ .70

TABLE 2. Analysis of variance for total germination, days to 50% of final germination, and abnormal germination for greasewood seeds incubated 14 days in NaCl-PEG and KCl-PEG solutions.

Source	Source of variation	Degrees of freedom	Osmotica	
			NaCl-PEG	KCl-PEG
			Total germination (%)	
North Harney	Osmotic potential (P)	3	14326.2*†	14694.9*
	Salt concentration (S)	4	40.3NS‡	55.8NS
	PXS	12	26.2NS	35.1NS
	Error	57	25.7	31.8
South Harney	P	2	23128.3*	21567.2*
	S	4	157.3*	291.6*
	PXS	8	48.2NS	54.6NS
	Error	42	57.9	45.5
Coyote Buttes	P	2	16519.4*	15247.3*
	S	4	389.7*	172.2*
	PXS	8	100.1*	50.5NS
	Error	42	39.1	36.7
			Days to 50% of final germination	
North Harney	P	3	189.3*	240.7*
	S	4	2.1NS	3.4NS
	PXS	12	2.5NS	2.5NS
	Error	57	2.9	2.2
South Harney	P	2	101.4*	134.3*
	S	4	3.6*	2.4*
	PXS	8	2.3NS	2.2NS
	Error	42	1.9	1.3
Coyote Buttes	P	2	130.1*	173.5*
	S	4	2.2NS	3.1NS
	PXS	8	1.6NS	1.9NS
	Error	42	3.2	1.3
			Abnormal germination (%)	
North Harney	P	4	36.8*	26.5*
	S	4	3.6NS	6.2NS
	PXS	16	6.1NS	7.4NS
	Error	72	6.7	5.1
South Harney	P	4	15.5*	32.7*
	S	4	2.0NS	3.2NS
	PXS	16	3.1NS	4.0NS
	Error	72	3.8	4.5
Coyote Buttes	P	4	37.7*	80.5*
	S	4	9.3NS	8.7NS
	PXS	16	8.1NS	7.2NS
	Error	72	6.7	5.7

†* F significant at the 0.05 level.
‡NS - Not significant at the 0.05 level.

TABLE 3. Regression equations and coefficients of determination for total germination, days to 50% of final germination, and abnormal germination for greasewood seeds incubated 14 days in NaCl-PEG and KCl-PEG solutions.

Seed source	Osmotica			
	NaCl-PEG		KCl-PEG	
	Regression equation	R^2	Regression equation	R^2
	Total germination (%)			
North Harney	$Y = 91.97+114.64X_1^{\dagger}+36.67X_1^2$	0.94	$Y = 93.56+116.77X_1+37.64X_1^2$	0.93
South Harney	$Y = 117.91+205.48X_1+89.36X_1^2-0.0001X_2^{\dagger}$	0.92	$Y = 115.52+198.52X_1+85.22X_1^2-0.0002X_2$	0.94
Coyote Buttes	$Y = 105.69+161.41X_1+61.42X_1^2-0.0004X_2-0.0003X_1X_2$	0.94	$Y = 91.89+127.97X_1+44.7X_1^2-0.0002X_2$	0.92
	Days to 50% of final germination			
North Harney	$Y = 2.4-5.5X_1$	0.65	$Y = 2.7-4.9X_1$	0.73
South Harney	$Y = 3.5-4.9X_1$	0.78	$Y = 3.2-5.1X_1$	0.81
Coyote Buttes	$Y = 3.7-5.0X_1$	0.80	$Y = 3.7-4.9X_1$	0.80
	Abnormal germination (%)			
North Harney	$Y = 4.94+1.30X_1$	0.31	$Y = 4.48+0.86X_1$	0.21
South Harney	$Y = 2.99+1.23X_1+0.05X_1^2$	0.37	$Y = 3.96+1.68X_1$	0.47
Coyote Buttes	$Y = 4.93+1.79X_1$	0.42	$Y = 6.06+2.61X_1$	0.58

[†] X_1 Osmotic potential (−MPa).
[‡] X_2 Salt concentration (μmol L^{-1}).

RESULTS

Percent seed fill was similar between collections (Table 1). Weights of sorted seeds were different, however, between collections, with the South Harney collection significantly ($p = 0.05$) heavier than the North Harney and Coyote Buttes collections.

Percent germination of the North Harney collection was related to osmotic potential in NaCl-PEG and KCl-PEG solutions, but salt concentration was not significant ($p = 0.05$) (Tables 2, 3). Seeds germinated at all osmotic potentials tested except −2.2 MPa (Table 4). Days to 50% of final germination were related to osmotic potential in both NaCl-PEG and KCl-PEG solutions (Tables 2, 3), increasing as osmotic potential decreased (Table 5). Some abnormal germination occurred at all osmotic potentials tested, and it decreased as osmotic potential declined (Tables 2, 3, 6).

Germination of the South Harney collection was reduced by declining osmotic potential and increasing NaCl and KCl concentrations (Tables 2, 3). Seeds germinated at −0.3 and −0.7 MPa, but no germination was observed at the lower osmotic potentials tested (Table 4). Osmotic potential was the only factor that affected days to 50% of final germination as osmotic potential declined (Table 5). Some seeds germinated abnormally at all osmotic potentials tested, but germination was not significantly ($p = 0.05$) affected by salt concentration (Tables 2, 3); abnormal germination declined as osmotic potential decreased (Table 6).

In NaCl-PEG and KCl-PEG solutions, total germination of the Coyote Buttes collection was significantly ($p = 0.05$) affected by osmotic potential and salt concentration (Tables 2, 3), with osmotic potential causing the greatest reduction (Table 4). Some seeds germinated at all osmotic potentials tested except −1.6 and −2.2 MPa (Table 4). Days to 50% of final germination and abnormal germination were related only to osmotic potential (Tables 2, 3); days to 50% of final germination increased and abnormal germination decreased

TABLE 4. Estimates of total germination for greasewood seeds after 14 days of incubation in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration (µmol·L^{-1})	Osmotic potential (−MPa)			
			0.3	0.7	1.2	1.6
			%			
North Harney	NaCl	0-68480	60.9	29.7	7.2	2.4
	KCl	0-53640	61.9	30.3	7.6	3.1
South Harney	NaCl	0	64.3	17.9	0.0	0.0
		8560	63.4	17.0	0.0	0.0
		17120	62.6	16.1	0.0	0.0
		34240	60.9	14.4	0.0	0.0
		68480	57.4	11.0	0.0	0.0
	KCl	0	63.6	18.3	0.0	0.0
		6705	62.3	17.0	0.0	0.0
		13410	60.9	15.6	0.0	0.0
		26820	58.3	12.9	0.0	0.0
		53640	52.4	7.0	0.0	0.0
Coyote Buttes	NaCl	0	62.8	22.8	0.4	0.0
		8560	60.2	21.2	0.1	0.0
		17120	57.5	19.6	0.0	0.0
		34240	52.2	16.3	0.0	0.0
		68480	41.6	9.8	0.0	0.0
	KCl	0	56.8	23.4	1.9	0.0
		6705	55.4	22.1	0.6	0.0
		13410	54.1	20.8	0.6	0.0
		26820	51.4	18.1	0.0	0.0
		53640	46.0	12.7	0.0	0.0

TABLE 5. Estimates of days to 50% of final germination for greasewood seeds incubated for 14 days in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration (µmol·L^{-1})	Osmotic potential (−MPa)			
			0.3	0.7	1.2	1.6
			%			
North Harney	NaCl	0-68480	4.1	6.3	9.0	11.2
	KCl	0-53640	4.2	6.1	8.6	10.5
South Harney	NaCl	0-68480	5.0	6.9	9.4	–†
	KCl	0-53640	4.7	6.8	9.3	–
Coyote Buttes	NaCl	0-68480	5.2	7.2	9.7	–
	KCl	0-53640	5.2	7.1	9.6	–

†No seeds germinated at this osmotic potential.

TABLE 6. Estimates of abnormal germination for greasewood seeds incubated for 14 days in NaCl-PEG and KCl-PEG solutions. Regression equations used to predict values are presented in Table 3.

Seed source	Osmotica	Salt concentration (µmol·L^{-1})	Osmotic potential (−MPa)				
			0.3	0.7	1.2	1.6	2.2
			%				
North Harney	NaCl	0-68480	4.6	4.0	3.4	2.9	2.1
	KCl	0-53640	4.2	3.9	3.4	3.1	2.6
South Harney	NaCl	0-68480	2.6	2.2	1.6	1.2	0.5
	KCl	0-53640	3.5	2.8	1.9	1.3	0.3
Coyote Buttes	NaCl	0-68480	4.4	3.7	2.8	2.1	1.0
	KCl	0-53640	5.3	4.2	2.9	1.9	0.3

as osmotic potential declined (Tables 5, 6).

Discussion

The differences in germination observed in this study may be attributed to genetics of the populations, environmental conditions, or both. It was not possible to separate their effects in this study. Regardless of which factor influenced germination, there were inter- and intrapopulation differences in responses to osmotic potential and concentrations of NaCl and KCl.

Germination of all populations was primarily reduced by osmotic potential, but germination in a portion of the South Harney and Coyote Buttes collections was reduced by increasing NaCl and KCl concentrations. Sensitivity to osmotic potential, rather than specific ions, may be important for survival since seeds are exposed to myriad combinations of ions under field conditions (Ungar 1982). Sensitivity to osmotic potential may be an adaptation that limits most germination to periods when salts are diluted or leached and conditions are favorable for seedling growth. In the Great Basin, soil water potentials are highest and salinity is lowest in the spring because salts are diluted or leached by winter precipitation (Roundy 1984).

On sites where seeds were collected for this germination study, greasewood seedlings were observed only during spring. Because Glenn and O'Leary (1984) found that growth of young greasewood plants decreased directly in response to increasing salinity, and because we found that water stress reduced and slowed germination, we hypothesize that most seeds of greasewood germinate when soil moisture is high for extended periods. This adaptation may maximize the time for growth of seedlings. Similar regeneration adaptations have also been suggested for other species in the Great Basin (Wood et al. 1976, Young and Evans 1981, Cluff et al. 1983, Roundy 1985).

Comparison of results in this study with previously published studies on greasewood germination suggests the possibility of geographical ecotypic differentiation. Sabo et al. (1979) reported a New Mexico collection of greasewood germinated 80% or more at osmotic potentials ranging from 0 to −1.6 MPa. Seeds collected in eastern Montana germinated at osmotic potentials as low as −3.6 MPa (Romo and Eddleman 1985). Furthermore, Romo and Eddleman (1985) reported that Na_2SO_4 and NaCl stimulated germination rate and total germination in greasewood, but germination of these collections from Oregon was either unaffected or reduced by NaCl and KCl. These southeastern Oregon collections germinated only at osmotic potentials of −1.6 MPa or higher, and germination was less than 30% at osmotic potentials lower than −0.3 MPa. Failure to germinate at low osmotic potentials and high salt concentrations may act to preserve a portion of the seed population and condition them for germination over a wider range of ensuing environmental conditions (Hegarty 1978, Ungar 1978).

Responses to osmotic potential and specific ions are only two factors to consider when characterizing the germination ecology of greasewood. Germination of these southeastern Oregon collections of greasewood was primarily limited by availability of water and, to a lesser degree, by specific ions. Germination under field conditions is, however, probably quite different from laboratory results because of interacting effects of climatic and edaphic factors.

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BIG SAGEBRUSH (*ARTEMISIA TRIDENTATA VASEYANA*) AND LONGLEAF SNOWBERRY (*SYMPHORICARPOS OREOPHILUS*) PLANT ASSOCIATIONS IN NORTHEASTERN NEVADA

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Abstract.—*Artemisia tridentata/Symphoricarpos oreophilus* and *Symphoricarpos oreophilus/Artemisia tridentata* plant associations were studied in northeastern Nevada. A 60-stand reconnaissance followed by a detailed study of 37 stands differentiated five important habitat types using an association table approach. Data reduction with DECORANA and TWINSPAN also described five plant associations that were differentiated by species occurrence and geographical distribution. All stands were found at elevations between 2,200 and 3,100 m in areas where snow accumulates and is late to melt. Stands are found on 15 families of soils that are relatively deep, often skeletal, dark colored, and productive. The dominant perennial grasses included *Agropyron spicatum*, *Agropyron trachycaulum*, and *Festuca idahoensis*.

Shrubby members of the genus *Artemisia* (sagebrush) comprise a significant portion of the vegetation in the Great Basin. Sagebrush gives the dominant aspect to vegetation over a wide range of altitude, climate, geological substrate, soils, and associated plant species. This environmental variability has resulted in a number of species, subspecies, and forms. In addition, a certain amount of hybridization has, no doubt, resulted in the existence of many ecotypes not yet defined (Beetle 1960, Winward and Tisdale 1969, and McArthur 1978).

Big sagebrush (*Artemisia tridentata*) is the most widely distributed and abundant species of the genus. Three subspecies have been identified, ssp. *vaseyana*, ssp. *tridentata*, and ssp. *wyomingensis*. Extensive stands of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) occur in central and northern Nevada in high-producing plant communities at high elevations. This study was limited to stands with either *Artemisia tridentata vaseyana* or snowberry (*Symphoricarpos oreophilus*) as the dominant or co-dominant shrub.

The objective of this study was to characterize the vegetation, topography, and soils of some *A. tridentata/S. oreophilus* habitat types in northeastern Nevada.

Methods

This study was confined to mountainous areas in northeastern Nevada where *Artemisia tridentata vaseyana* and *Symphoricarpos oreophilus* are locally abundant. The overall climate is primarily arid (Hunt 1967), although semiarid to subhumid conditions exist in many of the mountain ranges.

Mountain brush vegetation dominated by shrubs of these two species was studied by first selecting 60 stands in 18 mountain ranges in Elko, Eureka, Humboldt, Lander, Lincoln, Nye, and White Pine counties for a detailed reconnaissance. The plotless reconnaissance procedure outlined by Poulton and Tisdale (1961) was used to collect general vegetation information. A stand was selected for sampling if it was homogeneous with respect to species composition and dominance and had uniform relief of the soil surface. Transitional areas were avoided. For each stand, species were listed under three categories (tree, shrub, or herb physiognomic layer) and given both cover class and dominance ratings.

Physiographic features of percent slope, slope aspect, position of the stand on the slope, elevation, land form, and microrelief of the soil surface were recorded. Soil profile features noted were horizons, solum depth, gross differences in the texture and structure, and quantity of gravel and stone. Percent cover for stone, gravel, bare soil surface, and cryptogams was estimated.

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Based on results of this reconnaissance, 37 stands of vegetation in eight mountain ranges in Elko and White Pine counties were selected for more detailed study (Fig. 1). The stands selected were considered most nearly representative of the potential natural vegetation based on the absence of recent disturbance such as excessive grazing, wildfire, and accelerated erosion, and on a high proportion of grasses in the herb layer, particularly species of *Agropyron, Festuca,* and *Poa.* All stands were grazed by livestock during the summer months. Studies of relict and excellent condition sagebrush vegetation in other portions of the Great Basin have shown that grasses, particularly of the genera mentioned, comprised a dominant portion of the herb layer (Blackburn 1967, Blackburn et al. 1968b, c, 1969a, b, c, 1971, Passie and Hugie 1962, Tisdale et al. 1965, Zamora and Tueller 1973).

At each study site a homogeneous stand of vegetation was selected for sampling. Plant and ground cover data were collected on one 15- x 30-m macroplot located with the long axis oriented up and down slope. The right-hand boundary formed the baseline. Ten 15-m transects were located perpendicular to the baseline with five transects randomly placed in each half of the macroplot. Rooted frequency of all species was determined in 10 3- x 6-dm microplots placed at 1-m intervals along each transect line. Percent basal area of herbaceous species was estimated in 10 3- x 6-dm microplots on 4 of the 10 frequency transects. Two wire rings, one 5% and the other 2% of the microplot area, were used as an aid in estimation. Basal areas of 1 to 10% were estimated to the nearest 1%; those greater than 10% were estimated to the nearest 5%. Basal area for mat-forming species was considered as the total area encompassed by the periphery of the mat. Dead centers of bunchgrass were excluded from the cover estimate if they exceeded 1%.

Ground cover was estimated using the two outside corners of the microplot frame as points. Features recorded were basal area of plants, litter, cryptogam, bare soil surface, gravel (2-mm to 7-cm diameter), and stone (greater than 7-cm diameter). Percent cover was calculated from 200 points on each macroplot.

Shrub characteristics were evaluated on 15 1-m^2 microplots placed consecutively on the four transect lines to determine basal area of herbs. Shrub crown cover was estimated to the nearest 1% if less than 25% and the nearest 5% if greater than 25%. A wire ring equaling 5% of the microplot was used as an estimation. Openings in the shrub canopy greater than 2% were excluded from the cover estimate. Shrub density was obtained by counting individuals rooted in each microplot. The counts were summarized as numbers per 60 m^2. Shrub heights in each microplot were measured to the nearest centimeter.

A soil profile description was made at each macroplot location. Samples from the A1 and B2 horizons were analyzed for soluble salts, pH, and organic carbon.

Percent frequency and cover data were summarized in stand tables, and the resulting species groupings were used to make a subjective interpretation of the vegetation according to the association and habitat type ecological concepts. Final association interpretations were based on the dominant species in each plant layer. An association is defined as a plant community characterized by a definite floristic composition, physiognomy, and structure and growing under similar habitat conditions (Hanson and Churchill 1961). The associations are considered representative of potential native vegetation. A habitat type is defined as those geographic areas that support, or are capable of supporting, one association in the absence of disturbance (Daubenmire 1952). Habitat types are named by the characteristic climax plant association.

For objective analysis of the data we used the Cornell Ecology and Systematics computer programs DECORANA (Hill 1979) and TWINSPAN (Hill 1979). DECORANA (detrended correspondence analysis) creates ordinations of samples and all species. Through a process of repeated averaging, sample scores on the first axis of the ordination are defined as the average of the scores of the species that occur in a sample. Graphs showing placement of species and samples in relation to significant ordination axes are used with eigenvalues (to show variability) to explain the axes as ecological gradients. Each of the first three DECORANA ordination axes were analyzed by computing linear regression coefficients with the following stand parameters: elevations, radiation index (Frank and Lee 1966), shrub cover, grass cover, forb

TABLE 1. *Artemisia tridentata vaseyana/Symphoricarpos oreophilus* associations characterized in northeastern Nevada.

Associations	Number of stands sampled	Elevational range of stands (m)
Artemisia tridentata-Symphoricarpos oreophilus/Agropyron spicatum	14	2378-3010
Artemisia tridentata-Symphoricarpos oreophilus/Agropyron trachycaulum	6	2592-2713
Artemisia tridentata-Symphoricarpos oreophilus/Festuca idahoensis	5	2531-2592
Symphoricarpos oreophilus/Artemisia tridentata/Argropyron spicatum	10	2287-3003
Symphoricarpos oreophilus/Artemisia tridentata/Festuca idahoensis	2	2470

cover, total cover, number of species, latitude, and longitude. TWINSPAN (two-way indicator species analysis) successively splits the ordination of all the samples into halves and identifies indicator species for each division. The divisions are arranged in the printout in order showing the closeness of similarity between groups based on all species. The result is a classification of similar stands with the tightness of the groupings indexed by the eigenvalue of the division. The resulting classifications for both association tables and multivariate approaches were compared. We wanted to know if the multivariate approach, emphasizing all species equally, would describe plant associations readily identifiable in the field and potentially useful to resource managers.

RESULTS

Reconnaissance

Reconnaissance data allowed us to identify 15 mountain brush communities based on dominant species in the shrub and herb layer:

(1) *Artemisia tridentata–Symphoricarpos oreophilus/Agropyron spicatum*
(2) *Artemisia tridentata–Symphoricarpos oreophilus/Chrysothamnus viscidiflorus*
(3) *Artemisia tridentata–Symphoricarpos oreophilus/Chrysothamnus viscidiflorus/Agropyron spicatum*
(4) *Artemisia tridentata–Symphoricarpos oreophilus/Festuca idahoensis*
(5) *Artemisia tridentata–Symphoricarpos oreophilus/Poa sandbergii*
(6) *Artemisia tridentata–Symphoricarpos oreophilus/Stipa comata*
(7) *Artemisia tridentata–Purshia tridentata/Agropyron spicatum*
(8) *Artemisia tridentata–Purshia tridentata/Festuca idahoensis*
(9) *Artemisia tridentata–Cercocarpos ledifolius/Agropyron spicatum*
(10) *Artemisia tridentata–Chrysothamnus viscidiflorus/Agropyron spicatum*
(11) *Symphoricarpos oreophilus–Artemisia tridentata/Agropyron spicatum*
(12) *Symphoricarpos oreophilus–Artemisia tridentata/Agropyron trachycaulum*
(13) *Symphoricarpos oreophilus–Artemisia tridentata/Festuca idahoensis*
(14) *Symphoricarpos oreophilus–Artemisia tridentata/Poa sandbergii*
(15) *Symphoricarpos oreophilus–Artemisia tridentata–Amelanchier pallida/Agropyron spicatum*

Provisional association names were given to groups of stands with the same dominant species, the same combination of dominant species, or similar estimated cover percentages of certain species. Similarities among site factors such as elevation, aspect, percent slope, position on slope, and some soil characteristics (texture, structure, and percent sand and clay) were used as additional classification criteria.

Some of these 15 communities were judged to be seral stages of major associations. Others were grouped into one of the five final designations and considered to be incidental variants. The remaining communities (8, 9, and 15) were excluded from the study because they did not fit the criteria selected for the detailed analysis.

Intensive Study

Knowledge gained during the reconnaissance suggested that intensive work be confined to five (5) *Artemisia tridentata vaseyana–Symphoricarpos oreophilus* associ-

TABLE 2. Average density (No.), height (Ht.), and crown cover (Cv) for shrubs of the mountain brush plant associations.

Species	Association														
	Artr-Syor/Agsp			*Artr-Syor/Agtr*			*Artr-Syor/Feid*			*Syor-Artr/Agsp*			*Syor-Artr/Feid*		
	No.[a]	Ht. cm[b]	Cv %[c]	No.	Ht. cm	Cv %	No.	Ht. cm	Cv %	No.	Ht. cm	Cv %	No.[a]	Ht. cm	Cv %
Amelanchier pallida	2	171	T[d]	—	—	—	—	—	—	e	67	T[d]	—	—	—
Artemisia tridentata (Artr)	59	67	23	73	75	26	61	69	30	49	60	17	83	72	15
Berberis repens	—	—	—	e	5	T	—	—	—	—	—	—	1	3	T
Chrysothamnus viscidiflorus	16	19	2	18	27	2	24	30	2	28	29	5	35	34	4
Gutierrezia sarothrae	e	12	T	—	—	—	—	—	—	—	—	—	—	—	—
Pontentilla glandulosa	—	—	—	e	34	T	—	—	—	—	—	—	—	—	—
Prunus virginiana	e	25	T	—	—	—	—	—	—	—	—	—	—	—	—
Purshia tridentata	2	63	T	e	58	T	—	—	—	—	—	—	—	—	—
Ribes velutinum	—	—	—	—	—	—	—	—	—	5	33	T	—	—	—
Rosa woodsii	e	31	T	—	—	—	—	—	—	e	31	T	—	—	—
Symphoricarpos oreophilus (Syor)	322	43	17	118	36	14	311	39	18	394	33	21	259	43	22
Tetradymia canescens	e	28	T	—	—	—	—	—	—	—	37	T	—	—	—

a - Number per 60 m^2
b - Average height (cm) values calculated for stands in which individuals occurred
c - Average canopy cover percentage for a square meter
d - Cover values less than 1% indicated as *T*
e - Average density value less than 1
Agtr = *Agropyron trachycaulum*; Agsp = *Agropyron spicatum*; Feid = *Festuca idahoensis*

TABLE 3. Constancy (Cn), frequency (Fr), and herb basal area (Cv) for species in the *Artemisia tridentata vaseyana/Symphoricarpos oreophilus* associations.

Species[a]	*Artemisia tridentata vaseyana-Symphoricarpos oreophilus-Agropyron trachycaulum*			*Artemisia tridentata vaseyana-Symphoricarpos oreophilus-Festuca idahoensis*			*Artemisia tridentata vaseyana-Symphoricarpos oreophilus-Agropyron spicatum*		
SHRUBS	Cn	Fr	Cv	Cn	Fr	Cv	Cn	Fr	Cv
Amelanchier pallida	—	—	—	—	—	—	60	1	—
Artemisia tridentata	100	35	—	100	27	—	100	14	—
Chrysothamnus viscidiflorus	100	7	—	100	11	—	100	0	—
Purshia tridentata	—	—	—	40	1	—	—	—	—
Symphoricarpos oreophilus	100	10	—	100	5	—	100	8	—
HERBS (Grasses)									
Agropyron spicatum	33	1	T[b]	100	6	0.2	100	6	1.5
Agropyron trachycaulum	100	4	2.1	40	3	0.5	—	—	—
Bromus carinatus	17	1	0.1	—	—	—	—	—	—
Bromus marginatus	17	1	T	—	—	—	—	—	—
Bromus tectorum	67	2	T	80	5	0.3	87	4	0.1
Festuca idahoensis	83	6	1.0	100	5	2.7	47	3	0.3
Poa secunda	100	7	1.0	60	2	1.0	93	2	T[b]
Sitanion hystrix	17	2	T	—	—	—	—	—	—
(Forbs)									
Achillea millifolium	—	—	—	40	5	T	80	2	T
Agastache urticifolia	—	—	—	—	—	—	13	2	T
Agoseris glauca	33	6	0.1	60	3	T	33	2	T
Astragalus beckwithii	33	1	T	—	—	—	—	—	—
Balsamorhiza sagittata	50	4	T	40	2	T	80	5	T
Collinsia parviflora	100	9	0.4	100	9	0.3	73	3	0.3
Comandra pallida	—	—	—	40	2	T	—	—	—
Crepis acuminata	100	10	T	100	10	0.4	100	6	0.2
Eriogonum ovalifolium	50	2	0.3	—	—	—	27	1	T
Lupinus caudatus	100	12	0.2	100	15	1.2	100	7	0.4
Mertensia oblongifolia	83	9	0.2	100	8	0.4	100	8	0.3
Myosotis scorpioides	—	—	—	—	—	—	20	2	T
Penstemon hymilis	50	1	T	80	2	T	87	3	T
Phlox longifolia	33	1	T	60	9	0.1	27	2	T
Viola beckwithii	100	7	T	—	—	—	—	—	—

a - Only species with frequencies of 1% or greater in the 3- x 6-dm microplot are shown.
b - Average basal area less than 0.1% is indicated by T.

TABLE 4. Constancy (Cn), frequency (Fr), and herb basal area (Cv) for species in the *Symphoricarpos oreophilus/Artemisia tridentata vaseyana* associations.

Species[a]	*Symphoricarpos oreophilus-Artemisia tridentata vaseyana-Agropyron spicatum*			*Symphoricarpos oreophilus-Artemisia tridentata vaseyana-Festuca idahoensis*		
SHRUBS	Cn	Fr	Cv	Cn	Fr	Cv
Amelanchier pallida	22	1	—	—	—	—
Artemisia tridentata	100	17	—	100	16	—
Chrysothamnus viscidiflorus	100	21	—	100	12	—
Ribes velutinum	56	5	—	—	—	—
Symphoricarpos oreophilus	100	8	—	100	9	—
HERBS (Grasses)						
Agropyron spicatum	100	9	2.1	—	—	—
Agropyron trachycaulum	—	—	—	40	2	0.1
Bromus tectorum	89	4	0.1	100	8	0.2
Festuca idahoensis	78	6	T[b]	100	54	1.31
Melica bulbosa	11	1	T	—	—	—
Poa secunda	100	15	0.7	100	2	2.0
Stipa thurberiana	11	4	T	—	—	—
(Forbs)						
Achillea millifolium	33	2	T	—	—	—
Agoseris glauca	78	19	0.3	—	—	—
Aster scopulorum	67	4	T	—	—	—
Balsamorhiza sagittata	89	4	0.1	50	4	T
Collinsia parviflora	100	11	1.1	100	4	0.3
Crepis acuminata	89	8	0.2	100	6	0.1
Delphinium andersoni	78	4	T	—	—	—
Eriogonum ovalifolium	11	3	T	—	—	—
Geranium viscossium	11	2	T	—	—	—
Hydrophyllum capitatum	67	3	T	50	10	0.2
Lomatium cous	44	1	T	—	—	—
Lapinus caudatus	100	7	0.3	100	9	0.8
Mertensia oblongifolia	89	9	0.7	100	10	0.3
Penstemon humilis	89	4	0.1	—	—	—
Phlox longifolia	78	4	T	—	—	—
Senecio canus	67	7	T	—	—	—
Viola beckwithii	22	2	T	100	4	0.1

a - Only species with frequencies of 1% or greater in the 3- x 6-dm microplot are shown.
b - Average basal area less than 0.1% is indicated by *T*.

ations only (Table 1). These associations have the widest distributions and greatest abundance among the mountain brush plant associations of northern and central Nevada. These associations are described below, followed by the description and interpretation of the multivariate analysis. Data describing each plant association come from an association table which is on file at the University of Nevada, Reno. Vegetation characteristics for the five associations are presented in Tables 2, 3, and 4.

***Artemisia tridentata vaseyana–Symphoricarpos oreophilus/Agropyron spicatum* Association.**—This association is widely distributed throughout northern Nevada. Stands are located in mountainous terrain (2,378–3,010 m) in concave snowpockets on 16 to 31% slopes with predominantly northern aspects. Species composition of this association is very similar among stands in Elko County. Stands from White Pine County show greater variability.

The diagnostic characteristic of this association is the dominance of *Artemisia tridentata* in the shrub layer and of *Agropyron spicatum* in the herb layer. The average density of *Artemisia tridentata* (59 plants/60 m^2) is the lowest of the three associations with *A. tridentata* the dominant shrub (Table 3). *Artemisia tridentata* constitutes 55% of the total shrub crown cover, whereas *Symphoricarpos oreophilus* makes up 40% of the cover. *Symphoricarpos oreophilus* always has a high density but a low cover (Table 2). The average

TABLE 5. Soil surface characteristics for the associations dominated by *Artemisia tridentata vaseyana* or *Symphoricarpos oreophilus*.

	Soil surface characteristics					
Association	Plant cover %	Litter cover %	Bare soil surface %	Gravel cover %	Stone cover %	Cryptogam cover %
Artemisia tridentata-Symphoricarpos oreophilus/ Agropyron spicatum						
Average	39	32	19	7	2	Trace
Range	21–49	20–47	5–30	1–13	0–5	0–2
Artemisia tridentata-Symphoricarpos oreophilus/ Agropyron trachycaulum						
Average	36	27	24	9	2	2
Range	29–41	15–40	16–34	0–18	0–7	0–6
Artemisia tridentata-Symphoricarpos oreophilus/ Festuca idahoensis						
Average	42	39	15	2	Trace	2
Range	34–48	21–46	4–34	0–9	0–2	0–2
Symphoricarpos oreophilus Artemisia tridentata/ Agropyron spicatum						
Average	42	31	15	7	Trace	Trace
Range	37–47	17–48	8–26	1–12	0–2	0–2
Symphoricarpos oreophilus Artemisia tridentata/ Festuca idahoensis						
Average	41	36	14	6	2	1
Range	37–45	21–50	3–26	1–12	0–4	0–2

height of *A. tridentata* varies from 55 to 75 cm. *Chrysothamnus viscidiflorus* is 100% constant but contributes little to total plant cover. Eight other shrub species are found in these stands.

Four grass species and 12 forb species are found in this plant association (Table 3). Basal area and frequency of *Agropyron spicatum* is much greater than for any other herb in all stands. This species constitutes 79% of the total grass basal area and 48% of the total basal area of the herb vegetation. *Festuca idahoensis* and *Lupinus caudatus* are subdominant species in the herb layer. Total basal area of forbs is the lowest among all associations and is the most variable vegetation characteristic among stands in this association. Forbs with high constancy are *Archillea millifolium*, *Balsamorhiza sagittata*, *Collinsia parviflora*, *Crepis acuminata*, *Delphinium andersonii*, *Lupinus caudatus*, *Mertensia oblongifolia*, and *Penstemon humilis*. *Viola beckwithii* is highly constant among the stands in White Pine County but absent in the Elko County stands. *Lithospermum ruderale* is a characteristic species of stands in the northern Ruby Mountains and Jarbidge areas but is absent in White Pine County.

Basal plant cover and litter cover are comparatively high, 39% and 32% respectively (Table 5). The bulk of the litter occurs underneath and around the periphery of shrub crowns and consists primarily of leaf material from the shrubs, particularly *A. tridentata* and *S. oreophilus*. Few plants occur underneath the crown of *A. tridentata*, but nearly always plants of several species grow underneath the canopy of *S. oreophilus*.

TABLE 6. List of soil families supporting *Artemisia tridentata vaseyana* and *Symphoricarpos oreophilus* plant associations.

Soil family	Artr-Sylo/ Agsp %	Artr-Sylo/ Agtr %	Artr-Sylo/ Feid %	Sylo-Artr/ Agsp %	Sylo-Artr/ Feid %
Argic Cryoboroll, clayey over sandy or sandy-skeletal, montmorillonitic	27	—	—	—	—
Argic Cryoboroll, fine-loamy, mixed	—	—	20	—	—
Argic Pachic Cryoboroll, clayey over sand or sandy-skeletal, montmorillonitic	—	16	—	—	—
Argic Pachic Cryoboroll, fine-loamy, mixed	13	17	20	22	—
Argic Pachic Cryoboroll, fine-loamy over sandy or sandy-skeletal, mixed	—	17	—	—	—
Argic Pachic Cryoboroll, fine, montmorillonitic	—	—	—	45	—
Mollic Cryoboralf, clayey over sandy or sandy-skeletal, montmorillonitic	—	—	—	—	—
Mollic Cryoboralf, fine-loamy, mixed	20	33	20	11	50
Mollic Cryoboralf, fine, montmorillonitic	13	—	20	—	—
Mollic Cryoboralf, fine-loamy over sandy or sandy-skeletal, mixed	13	—	—	—	—
Ochreptic Cryoboralf, loamy, mixed	7	—	—	—	—
Typic Cryoboralf, fine-loamy, mixed	—	17	—	—	—
Typic Cryoboralf, fine-loamy over sandy or sandy or sandy-skeletal, mixed	—	—	—	—	50

Agsp = *Agropyron spicatum*
Agtr = *Agropyron trachycaulum*
Artr = *Artemisia tridentata*
Feid = *Festuca idahoensis*
Sylo = *Symphoricarpos oreophilus*

Soils are largely cryoborolls or cryoboralfs; 27% are Agric Cryoborolls, while 53% are one of four families of Mollic Cryoboralfs (Table 6). Many of the soils have dark brown to dark reddish brown, sandy loam and clay loam, angular and subangular blocky argillic horizons. Average solum gravel content varies from 10 to 30%. Thickness of the solum ranges from 42 to 98 cm. Most of the soils have fine-loamy textures (Table 7). Surface soils generally have low gravel and stone cover and small amount of bare soil (19%) due to high plant and litter cover.

***Artemisia tridentata vaseyana–Symphoricarpos oreophilus/Agropyron trachycaulum* Association.**—Stands representing this association are located in the Schell Creek Range, Ward Mountain, and Mt. Moriah areas of White Pine County with one stand in Elko County. All are located in mountainous terrain on concave to gently convex slopes with northeastern and northwestern aspects. Slopes range from 12 to 38%, and elevations range from 2,592 to 2,713 m.

The dominance of *Artemisia tridentata* in the shrub layer and *Agropyron trachycaulum* in the herb layer characterize this association (Table 3). The average density of *A. tridentata* (73 plants/60 m^2) is next to the highest of all associations studied (Table 3). Average cover of *A. tridentata* (26%) is 62% of the total shrub crown cover. *Symphoricarpos oreophilus* cover (14%) constitutes 33% of cover. The average density of *S. oreophilus* (181 plants/60 m^2) is the lowest among the associations studied (Table 3). Shrubs of secondary importance are *Chrysothamnus viscidiflorus* and *Purshia tridentata*.

Fourteen grass species constitute 78% of a total grass basal area of 4.2%. Basal area of *Agropyron trachycaulum* (2.1%) constitutes 50% of the total grass basal area and 39% of the basal area of all vegetation (5.4%). *Festuca idahoensis* and *Poa sandbergii* are subdominant species. The forb component (22 species) is very similar in composition to that of the *Artemisia tridentata vaseyana–Symphoricarpos longiflorus/Festuca idahoensis* association. Characteristic species with 50% constancy are *Collinsia parviflora*, *Crepis acuminata*, *Lupinus caudatus*, *Balsamorhiza sagittata*, *Eriogonum ovalifolium*, *Mertensia oblongifolia*, and *Penstemon humillis* (Table 3).

Combined plant and litter cover accounts for 63% of the soil surface cover. The amount

Table 7. Summary of textural classes[a] and diagnostic horizons of soils supporting stands of *Artemisia tridentata* and *Symphoricarpos oreophilus*.

Associations and number of stands sampled	Soil family texture class in control section						Diagnostic horizons			
							Epipedons		Subsurface horizons	
	Coarse-loamy	Fine-loamy	Fine	Very fine	Loamy-skeletal	Clayey-skeletal	Mollic	Ochric	Argillic	Cambic
			%[b]				%		%	
Artr-Sylo/ Agsp (14)	—	47	13	—	7	33	40	60	93	7
Artr-Sylo/ Agtr (6)	—	67	—	—	16	17	67	33	83	17
Artr-Sylo/ Feid (5)	—	60	20	—	—	20	40	60	100	—
Sylo-Artr/ Agsp (10)	22	33	45	—	—	—	78	22	78	22
Sylo-Artr/ Feid (2)	—	100	—	—	—	—	—	100	50	50

a - Soil family textural classification in soil taxonomy (Soil Survey Staff 1975)
b - Percent of stands

Artr - *Artemisia tridentata*
Sylo - *Symphoricarpos longiflorus*
Agsp - *Agropyron spicatum*
Agtr - *Agropyron trachycaulum*
Feid - *Festuca idahoensis*

of bare soil (24%) is the highest of all associations, and gravel cover and stone cover are 9% and 2%, respectively (Table 5).

Soils are both cryoboralfs and cryoborolls (Table 6). The cryoborolls are all Argic Pachic Cryoborolls with fine-loamy to sandy-skeletal textures (Table 7). The epidedons are predominantly mollic, and most soils (83%) have argillic subsurface horizons. Average gravel content varies from 5 to 25%. Only one profile was found on bedrock (74 cm deep).

***Artemisia tridentata vaseyana–Symphoricarpos oreophilus/Festuca idahoensis* Association.**—Two of the stands representing this association are located on Spruce Mountain, two on Mt. Moriah, and one in Harrison Pass. Each stand occurs in mountainous terrain on 19 to 29% slopes with north, east, and west aspects and elevations of 2,531 to 2,592 m.

The vegetation is characterized by the dominance of *A. tridentata* in the shrub layer (Table 2) and *Festuca idahoensis* in the herb layer (Table 3). *Artemisia tridentata* cover of 30% constitutes 60% of the total shrub crown cover and has a density of 61 plants/60 m^2. *Symphoricarpos oreophilus* cover of 18% constitutes 36% of the total shrub crown cover and has a very high density (311 plants/60 m^2) (Table 3). *Chrysothamnus viscidiflorus* is one of four highly constant shrubs but contributes little to total crown cover.

The total grass basal area (4.7%) is composed almost entirely of *Festuca idahoensis* (2.7%) and *Poa sandbergii* (1.0%); *Agropyron trachycaulum* is a minor species. Only six grass species were found. *Festuca idahoensis* comprises 38% of the total herbaceous basal area and 58% of the total grass basal area. The total herbaceous basal area (7.1%) and the total grass basal area (4.7%) are the highest of the associations studied. The total forb basal area (2.4%) is the highest among *A. tridentata*–dominated stands. The forb component consists of 20 species. Species with 80% constancy or greater are *Collinsia parviflora*, *Crepis acuminata*, *Lupinus caudatus*, *Mertensia oblongifolia*, *Penstemon humilis*, and *Viola beckwithii*. The first four species are the most abundant.

Average plant basal area cover (42%) and litter cover (39%) are the highest of all associations studied (Table 5). Gravel, stone, and cryptogam cover is very low. The bare soil surface (15%) is intermediate for all associations studied but is the lowest with respect to other *A. tridentata*–dominated plant communities.

At least 60% of the soils are Mollic Cryoboralfs with a few Argic Pachic Cryoborolls (Tables 6, 7). All subsurface horizons are argillic, and ochric epipedons are common. The most common soil family textural class is fine-loamy (Table 7).

***Symphoricarpos oreophilus–Artemisia tridentata vaseyana/Agropyron spicatum* Association.**—This association occurs in the southern Schell Creek Range with three exceptions. Two stands are in the Jack Creek area of Elko County and one stand is on Spruce Mountain. Stands are found on 10 to 30% slopes with northerly aspects at elevations between 2,287 and 3,003 m.

Robust *Symphoricarpos oreophilus* shrubs and an herb layer dominated by *Agropyron spicatum* characterize the vegetation (Tables 2, 4). In addition, this association has less *A. tridentata* (17%) than did the first three associations described. *Symphoricarpos oreophilus* cover (21%) comprises 49% of the total shrub cover and has the highest shrub density (394 plants/60 m^2) of all associations studied. *Artemisia tridentata* constitutes 38% of the shrub crown cover but has a very low density (49 plants/60 m^2). Besides *S. oreophilus* and *A. tridentata*, *Chrysothamnus viscidiflorus* is the only other important shrub, although *Ribes velutinum* has a constancy of 5% (Table 4).

Agropyron spicatum and *Poa secunda* have 100% constancy in this association. Fourteen grass species were found. *Agropyron spicatum* cover (2.1%) comprises 41% of the total herbaceous basal area (5.9%) and 68% of the total grass basal area (3.1%). *Lupinus caudatus* and *Collinsia parviflora* have constancies of 100% and contribute 50% of the total forb basal cover (28%) for 32 forb species. *Mertensia oblongifolia* and *Agoseris glauca* have constancies of 89% and 78%, respectively, and contribute 40% of the average total forb basal area (Table 4). *Festuca idahoensis* and *Senecio canus* have low constancies but comprise a significant portion of the total forb basal area in some stands. Other forbs characteristic of this association are *Penstemon humilis*, *Crepis acuminata*, and *Balsamorhiza sagittata*.

Plant and litter cover combined (73%) is the lowest of the *S. oreophilus* plant associations and is related to the high bare soil surface percentage of 19% (Table 5). Gravel cover (7%) was next to the highest among all the associations, but stone and cryptogam cover was the lowest of all associations.

Nearly half of the soils are fine, montmorillonitic Argic Pachic Cryoborolls (Table 6). Another 22% are a fine-loamy, mixed family of the same soil subgroup.

***Symphoricarpos oreophilus–Artemisia tridentata vaseyana/Festuca idahoensis* Association.**—Two stands represent this association, one on Mt. Moriah and the other on Ward Mountain in White Pine County. These stands occur on 26 and 28% slopes, respectively, and with northeast and northwest aspects at about 2,470 m.

The vegetation is characterized by the dominance of *Symphoricarpos oreophilus* in the shrub layer and *Poa sandbergii* and *Festuca idahoensis* in the herb layer (Tables 2, 4).

The physiognomy of this association is quite distinct from other plant associations because of the lack of a noticeable sagebrush aspect. These sites are snowpockets and are obviously dominated by *S. oreophilus*, a dark green shrub generally lacking the dull gray appearance of *A. tridentata*. *Symphoricarpos oreophilus* has a high density and a cover (22%) that comprises 53% of the total shrub crown cover (Table 2).

The average total basal area of herbaceous vegetation (5.1%) and the average total grass basal area (3.3%) are comparatively low when compared with the other associations in this study. *Poa sandbergii* has 2% cover and *Festuca idahoensis* has 1% cover (Table 4). Neither grass is clearly dominant. The association was named after *Festuca idahoensis* because it is considered to be the dominant perennial grass on these sites. *Poa sandbergii* composes 61% of the total grass basal area and 40% of the total basal area of herbaceous vegetation. All other grass species have low basal area and frequency, except *Festuca idahoensis*. Forbs are sparse; only 23 species were found, and frequency percentages are low. The floristic structure of forbs resembles the *Artemisia tridentata vaseyana–Symphoricarpos oreophilus/Festuca idahoensis* association, which had both low forb constancy and frequency. Highly constant forbs are *Collinsia parviflora*, *Crepis acuminata*, *Mertensia oblongifolia*, *Lupinus caudatus*, and *Viola beckwithii*.

Bare soil surface is the lowest of the associations studied and results from a high plant and

TABLE 8. Number of stands sampled falling into either TWINSPAN groups or plant associations based on dominant species.

Plant associations	TWINSPAN group					
	C	E	B	D	A	Totals
Artr/Syor/Agsp	4	7	3	—	—	14
Syor/Artr/Agsp	—	2	1	—	7	10
Artr/Syor/Agsp	—	—	3	3	—	6
Syor/Artr/Feid	—	—	1	1	—	2
Artr/Syor/Feid	—	—	2	1	2	5
Totals	4	9	10	5	9	37

Artr = *Artemisia tridentata*
Agtr = *Agropyron trichophorum*
Feid = *Festuca idahoensis*
Syor = *Symphoricarpos oreophilus*
Agsp = *Agropyron spicatum*

litter cover. Gravel, stone, and cryptogam cover is very low. One soil is a fine-loamy to sandy-skeletal Typic Chryochrept and the other a mollic Cryoboralf (Table 7). Both soils are neutral in reaction with roots well distributed throughout the profile.

Multivariate Analysis

The TWINSPAN classification clearly did not separate the plant associations in the same way as did the associations table groupings which were based on the dominant shrub and the dominant perennial grass (Fig. 4, Table 8). The TWINSPAN dendrogram organized the study site into five groupings based on the similarity of occurrences of specific indicator species. These floristically based groups had specific geographic locations (Fig. 1). Their distribution, with only a few exceptions, is characterized by a north-south orientation and by association with specific mountain ranges. These results are an expression of the north-south environmental control of the indicator species delineated by the TWINSPAN analysis. Environmental controls are such that many groupings are found only on certain mountain ranges or only in the north or south part of the study area. The TWINSPAN groups were associated with one, two, or three plant associations with the exception of Group B which has representatives from each association (Table 8).

Group A is separated with the following indicator species: *Astragalus kentrophyta implexus*, *Hydrophyllum capitatum*, *Senecio canus*, *Astragalus* sp., and *Ribes velutinum*. *Elymus cinereus* and *Phlox longifolia* are also indicators but less definitive than those listed above. *Lithospermum ruderale* is conspicuous by its absence. These stands are found primarily at the southern end of the site distribution and have *Agropyron spicatum* as the dominant perennial grass. Aspects are northwest and are found at relatively high elevations, mostly above 2,800 m. These stands tend to be much drier than expected for their elevation with relatively low vegetation cover (43%).

Group B indicator species include *Agropyron trachycaulum* and *Sitanion hystrix*, although the latter species is not a strong preferential. *Phlox longifolia* tends to be absent as does *Delphinium andersonii*. These sites are found at intermediate elevations (mostly below 2,600 m) on northeast aspects and are probably drier than Group A. However, these stands had the highest total vegetation cover of all stands studied (65%).

Group C has the following species as indicators: *Eriogonum ovalifolium*, *Stipa comata*, *Collinsia parviflora*, and *Allium acuminatum*. *Agoseris glauca* and *Phlox longifolia* are noticeably absent. These stands are found in the south Ruby Mountains at elevations near 2,400 m. However, they are relatively moist sites, wetter than would be expected for the elevation.

Group D has *Astragalus calycosus*, *Berberis repens*, and *Myosotis scorpiodes* as indicator species. *Balsamorhiza sagittata* and *Agoseris glauca* tend to be absent from these stands. They tend to be average in terms of elevation (2,600 m) and moisture.

Group E indicators are *Calychortus elegans*, *Rosa woodsii*, and *Tetradymia canescens*. *Festuca idahoensis* is generally missing in these stands. *Elymus cinereus* is also important in this group of stands. They occur at relatively low elevations (< 2,500 m) in the northern part of the distribution (Fig. 1).

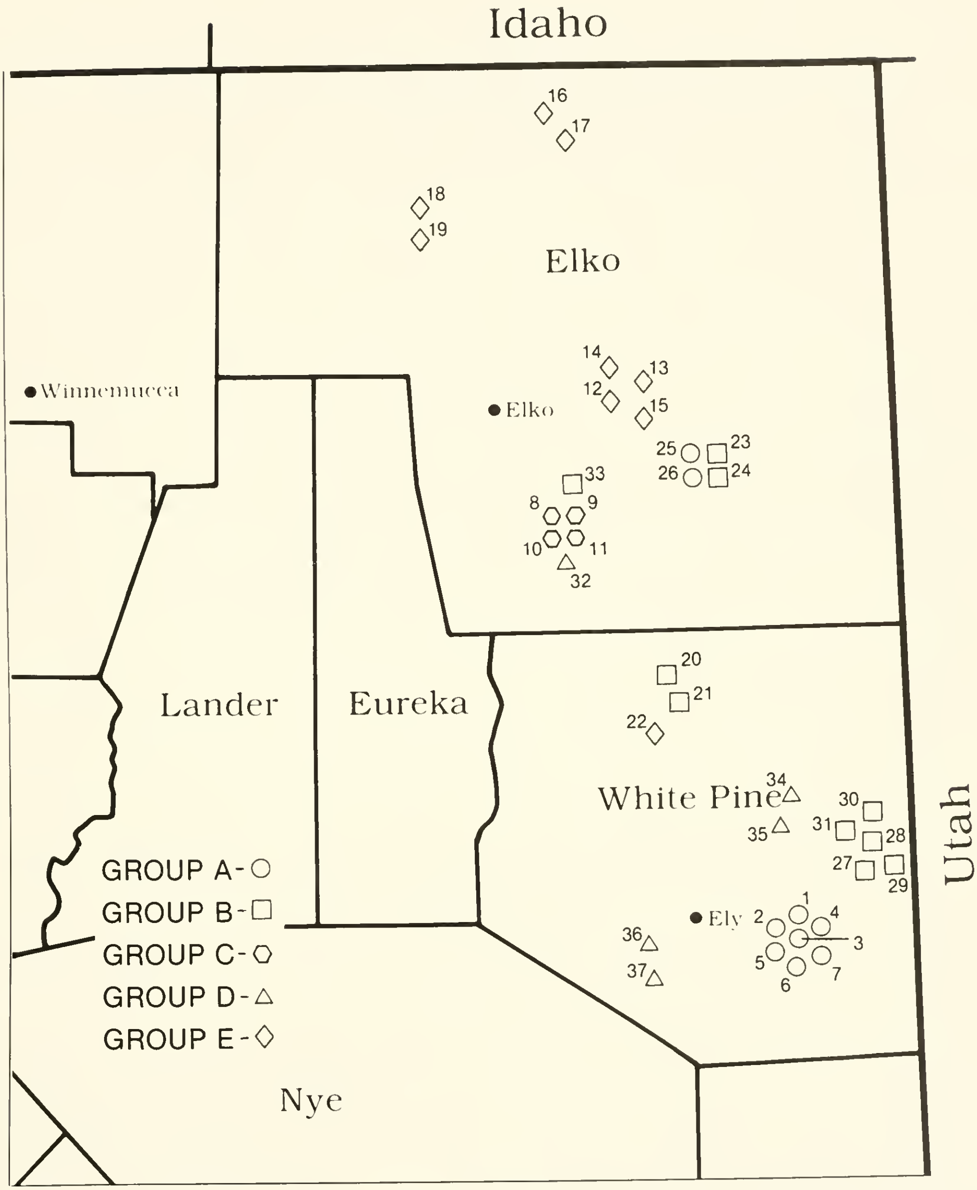
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Fig. 1. Location of detailed study sites in Elko and White Pine counties of northeastern Nevada. The group designations indicate the location of the five TWINSPAN groupings.

ther elucidate the environmental factors associated with distribution of these stands of vegetation. Axis 1 (Figs. 2, 3) is significantly correlated with decreasing latitude. A north-south distribution of the stands goes from approximately 41 degrees to 39 degrees North latitude. This axis is also significantly correlated with a significant reduction in the number of species/stand from 22 to 18.

Axis 2 (Fig. 2) represents a gradient significantly correlated with increasing elevation, higher solar radiation intensities, and a somewhat reduced number of species. Elevation along the gradient increases from 2,600 to 2,800 m. The radiation index increases from 42 to 45 with a very slight but significant reduction in the number of species.

The distribution of the Axis 3 standard devi-

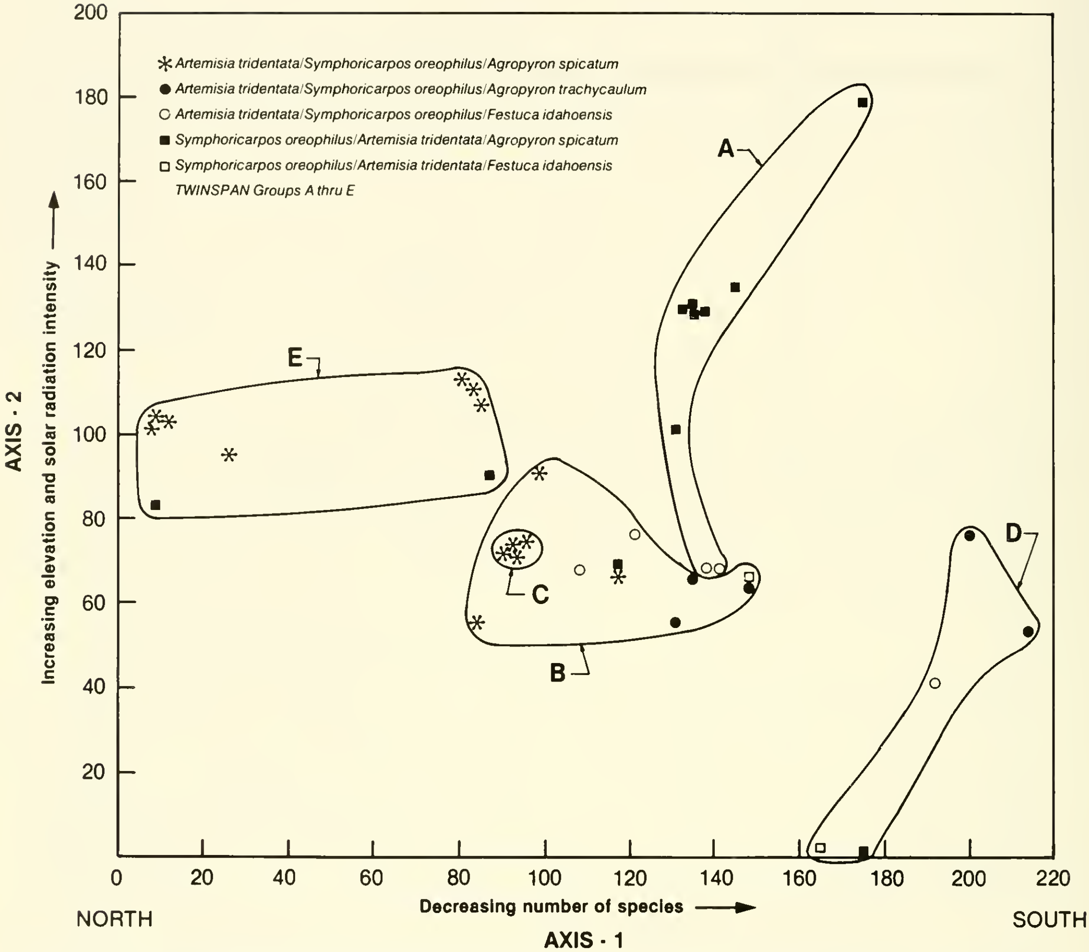

Fig. 2. DECORANA ordinations of Axis 1 and Axis 2 with separation of the five plant associations interpreted from the association table. Lines circle the TWINSPAN groups.

ations showed significant correlations with decreasing grass cover, shrub cover, and total vegetation cover along with an increase in the number of species per stand from 17.6 to 21.5. Grass cover decreased from 5.9 to 0.9%, shrub cover from 57.2 to 36.1%, and total vegetation cover from 65.7 to 37.6%.

Ordination of the 37 stands in this study showed significant relationships to environmental factors. The first axis (Axis 1) is related to latitude and species number in the stand and Axis 2 to elevation increases and the associated higher solar radiation intensities. Axis 3 is representative of a reduced level of shrub, grass, and total vegetation cover.

Further comparisons between the plant associations and the TWINSPAN groups show that the *Artemisia tridentata/Symphoricarpos oreophilus/Agropyron trichophorum* sites are found at southern locations within the study area and *Artemisia tridentata/Symphoricarpos oreophilus/Agropyron spicatum* stands are found further north. The other three plant associations are found at intermediate latitudes. Total vegetation cover was highest for *Artemisia tridentata/Symphoricarpos oreophilus/Festuca idahoensis* stands.

Soils

Soils associated with these mountain brush associations are primarily mollisols or alfisols, although two are inceptisols. Well over half have argillic horizons that are not restrictive to rooting. pH values are generally near neutral or slightly acidic. Epipedons are either ochric or mollic with a few more of the latter.

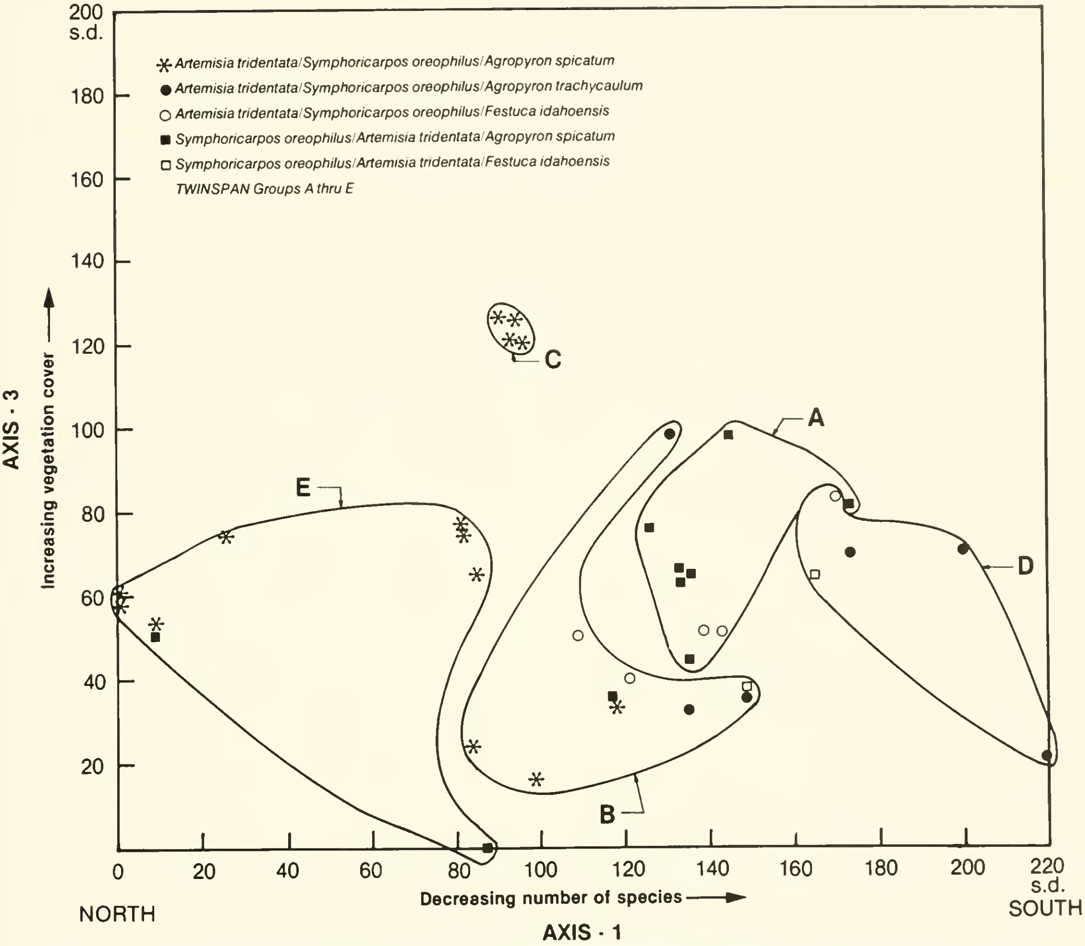

Fig. 3. DECORANA ordinations showing Axis 1 and Axis 3 with separation of the five plant associations interpreted from the association table. Lines circle the TWINSPAN groups.

The soil family textural classes are mostly fine-loamy, indicating good plant growth and rooting characteristics. Those soils that are clayey are also skeletal and indicate a good rooting medium (Table 7).

Soils supporting *Festuca idahoensis* have a deeper solum (A + B horizon) that averages 79 cm, while those soils supporting stands of either *Agropyron spicatum* or *Agropyron trachaycaulum* have a solum depth averaging only 68 cm. The *Festuca idahoensis* sites also have a higher litter cover, lower bare soil surface, and lower gravel and stone cover than do surface soils on the more xeric *Agropyron spicatum* and *Agropyron trachycaulum* associations. These soils are generally well drained, loamy, deep, sometimes rocky, and dark colored with many roots, no restrictive layers, and relatively high organic matter.

DISCUSSION

Mountain brush rangeland associations dominated by either *Artemisia tridentata vaseyana* or *Symphoricarpos oreophilus* have not been studied extensively. The works of Blackburn et al. (1968a, b, c, 1971a) list only a few such associations. Most studies of the ecology of *A. tridentata* vegetation have generally ignored these low-acreage, high-producing plant associations.

Blackburn et al. (1969a) described an *Artemisia tridentata/Symphoricarpos vaccinoides* association in western Nevada with 30% cover of *A. tridentata* and only 3% cover for *S. vaccinoides*. Blackburn et al. (1968a,

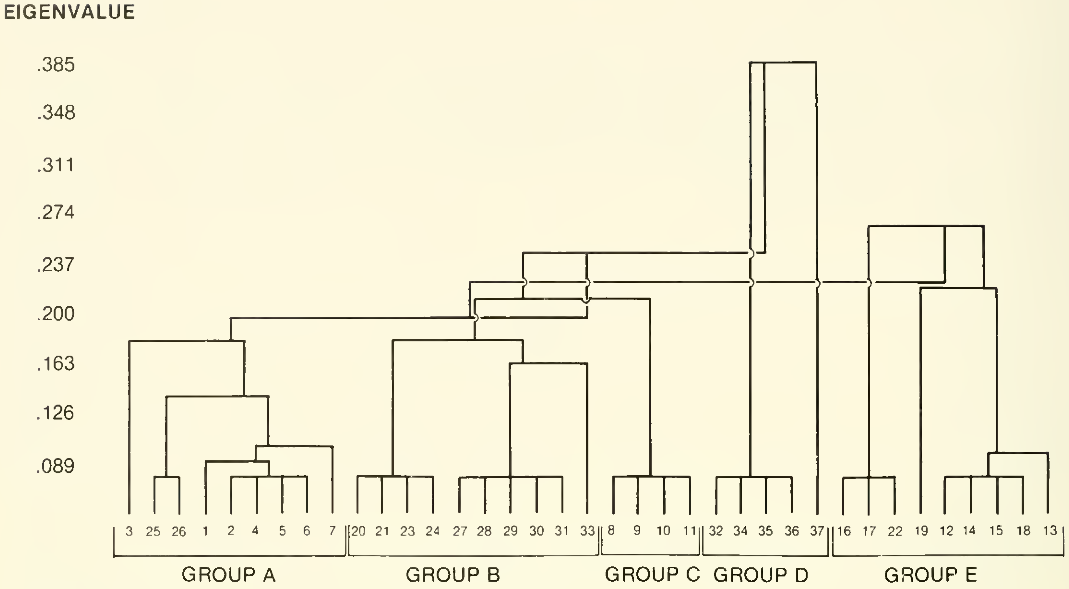

Fig. 4. TWINSPAN dendrology showing the separation of five groupings of the 37 study plots.

1971) described a low sagebrush association, *Artemisia longiloba/Poa sandbergii*, and an *Artemisia tridentata/Agropyron smithii/Poa nevadensis* association, both of which contain some *S. oreophilus*. Additionally, they described an *Artemisia tridentata/Symphoricarpos oreophilus/Agropyron spicatum* association with 16.3% cover for *Artemisia* and 15.6% cover for *Symphoricarpos*. The same association has 2.0% cover for *Agropyron spicatum* and 1.0% cover for *Festuca idahoensis*. Several low seral communities were described that have some *Symphoricarpos*. They were *Artemisia tridentata/Chrysothamnus viscidiflorus/Poa sandbergii/Wyethis mollis*, *Artemisia tridentata/Chrysothamnus viscidiflorus/Sitanion hystrix*, and *Artemisia tridentata/Poa sandbergii/Balsamorhiza sagittata*. Also they described an *Artemisia tridentata* (10.2% cover)/*Symphoricarpos oreophilus* (4.5%)/*Amelanchier pallida* (4.5%) association. Mooney (1985) recently described seven *Artemisia tridentata vaseyana* plant associations in the Great Basin. Many of these stands contain *Symphoricarpos oreophilus*.

Little biomass productivity data for these sites are available. However, their relatively greater number of species, deeper soils, and higher total ground cover lead to the conclusion that production is high for these communities relative to most other sagebrush-dominated plant associations. Both Daubenmire (1970) and Franklin and Dyrness (1969) described the *Festuca idahoensis/Symphoricarpos albus* habitat type. Daubenmire found that the total production of all vasculars was 30gm^{-2} while total grass production was 105m^{-2}.

The groupings differentiated with the TWINSPAN dendrogram, apart from Groups A and C, do not show a strong relationship with the subjectively determined associations based on dominant species. Group A includes primarily *Symphoricarpos oreophilus/Artemisia tridentata/Agropyron spicatum* plant associations. Group C is made up of the *Artemisia tridentata/Symphoricarpos oreophilus/Agropyron spicatum* plant association. The other groupings all show greater variability. This suggests that objective classification approaches based on presence and absence of all species may give classifications that differ substantially from those based on the presence of designated dominant species which were done here in the association table analysis.

The *Artemisia-Symphoricarpos* associations may represent a moisture gradient as one goes from high *Artemisia* to low *Symphoricarpos* and the reverse. They do represent relatively low-acreage, high-producing sites within the *Artemisia* vegetation.

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HABITAT AND COMMUNITY RELATIONSHIPS OF CLIFFROSE (*COWANIA MEXICANA* VAR. *STANSBURIANA*) IN CENTRAL UTAH

K. P. Price[1] and J. D. Brotherson[2]

ABSTRACT.—Cliffrose (*Cowania mexicana* var. *stansburiana* [Torr.] Jepson) community measurements were taken in central Utah. Data revealed a high between-site similarity of 78.5%. Soil analysis for sites showed most macronutrients, and some micronutrients, relatively low. Cover of cliffrose was found to increase with increases in soil magnesium ($p \leq 0.01$). Plants growing on the sites have adapted life cycles to exploit moisture and nutrients during seasons of maximum availability. Prevalent species in the community were cheatgrass (*Bromus tectorum*), cliffrose, madwort (*Alyssum alyssoides*), and bluebunch wheatgrass (*Agropyron spicatum*). Annual grasses were the most important life form to community composition; the second was shrubs. Ratios between soil nutrients and cliffrose tissue nutrients indicate active transport of some elements. Data indicated a steady decline in establishment of new cliffrose individuals on the sites since 1957. This lack of reproductive success is most likely due to a combination of factors but appears most influenced by the elevated levels of annual plants (mainly cheatgrass) on the sites. If the cliffrose communities in central Utah are to be maintained, special attention to their management must be considered and implemented.

Cliffrose (*Cowania mexicana* var. *stansburiana* [Torr.] Jepson) (McMinn 1939) is an evergreen shrub, a member of the rose family, and is found growing on dry, rocky slopes in the western United States (McArthur et al. 1983). The plant ranges from 1 to 4 m in height, but under favorable circumstances near the south rim of the Grand Canyon it becomes a small tree 6 to 8 m high (Dayton 1931, Blauer et al. 1975).

In central Utah it is characteristically found associated with limestone areas on west and southwest slopes at elevations between 1,200 and 2,400 m. Elsewhere, it is found on granitic, volcanic, and other igneous formations where it is most often associated with juniper, pinyon, mountain mahogany, serviceberry, sagebrush, live oak, and other moderately dry site (xerophytic) shrubs and small trees (U.S. Forest Service 1937). The geographical range of cliffrose reaches from western Colorado to California and from northern Utah to Mexico (McMinn 1939, McArthur et al. 1983).

Although its herbage has a bitter taste, cliffrose is a valuable browse species for many animals. On the Kaibab Plateau of northern Arizona, degree of twig use on cilffrose was, for many years, viewed as an indicator of hunting pressure needed to control the deer herds (McCulloch 1966). Since cliffrose is found mostly on low-elevation deer winter ranges, is evergreen, and stands above the snow and within reach to permit grazing, it is one of a few available food sources for deer during the critical winter period.

The importance of cliffrose as forage for both livestock and wildlife has stimulated studies dealing with its potential in range revegetation and in reclamation (McCulloch 1969 and 1971, Alexander et al. 1974, Plummer 1974, Giunta et al. 1975, Evans and Young 1977). Other studies have dealt with its utilization by deer and livestock and its response to browsing (Jensen and Scotter 1977, McCulloch 1978, Neff 1978, Jensen and Urness 1981).

Smith (1957) compared the nutritional value of cliffrose with other important range shrubs. His data show cliffrose to be average when compared with other shrubs. Welch et al. (1983) found cliffrose to have winter crude protein levels of 8.8% and winter in vitro digested dry matter contents of 36.7%. Both of these values rank well among comparable values for other winter forages.

Other works on cliffrose include seed germination (Piatt and Springfield 1973, Stevens et al. 1981, Young and Evans 1981), hybridization and introgression of cliffrose into bitterbrush (Stutz and Thomas 1963, Blauer et al. 1975, Koehler and Smith 1981,

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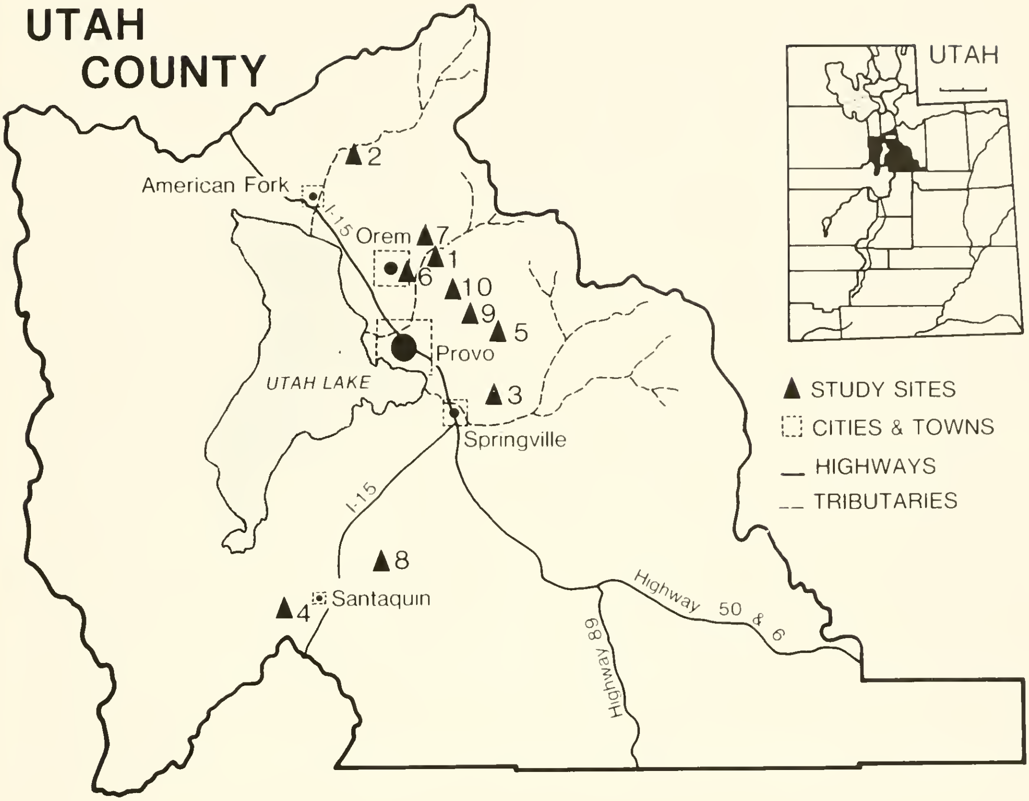

Fig. 1. A map of the study area (Utah County) in central Utah. The site names are: (1) Edgemont–Provo Canyon Junction; (2) American Fork Canyon; (3) Springville; (4) Santaquin; (5) Rock Canyon; (6) Provo River bottom; (7) Northern Provo Canyon; (8) Spring Lake; (9) Southern Indian Hills; and (10) Northern Indian Hills.

McArthur et al. 1983), secondary chemistry (Haynes and Holdsworth 1980) nitrogen-fixing ability (Righetti and Munns 1980, Nelson 1983, Righetti et al. 1968), and root morphology (Cline 1960).

A literature search revealed few studies addressing the ecology and habitat requirements of cliffrose. However, some studies were found dealing with the subject. Fairchild and Brotherson (1980) discussed the microhabitat relationships of six major shrubs in Arizona (which included cliffrose); Mortensen (1970) studied the ecological variations of leaf anatomy of apache plume (*Fallugia paradodoxa*), cliffrose, bitterbrush (*Purshia* sp.), and mountain mahogany (*Cercocarus* sp.); Stutz and Thomas (1964) and McArthur et al. (1983) studied habitat differences between antelope bitterbrush and Stansbury cliffrose; and Koehler and Smith (1981) described sites where desert bitterbrush and Stansbury cliffrose grow together with desert bitterbrush occupying slightly lower elevations.

Since cliffrose assumes a vital role in sustaining wildlife, and since there is a lack of studies dealing with its habitat relationships, this study of cliffrose was undertaken to further our understanding of its habitat requirements. Our objectives were to investigate the habitat and community relationships of cliffrose in central Utah where it is growing near the limit of its northern range (Cole 1982, McArthur et al. 1983) and to determine factors affecting its growth and establishment. This information should aid in the formulation of management plans to improve wildlife winter range.

Study Area

The study area, confined to central Utah (Fig. 1), is located along the west face of the

TABLE 1. Highs, lows, means, standard deviations, and coefficients of variation for abiotic factors associated with the cliffrose sites in central Utah.

Abiotic factors	High	Low	Mean	Standard deviation	Coefficient of variation
		General site factors			
% Gravel	62.0	30.0	48.7	10.3	21.1
% Sand	76.0	3.0	53.6	23.9	25.9
% Silt	41.0	15.0	27.9	8.5	30.5
% Clay	34.0	10.0	18.3	7.5	41.0
% Organic matter	7.1	2.5	4.8	1.6	33.3
Soil penetrability (cm)	28.0	9.0	17.9	7.4	41.3
Soluble salts	477.0	330.0	398.4	48.1	12.1
Aspect (degrees)	330.0	140.0	244.0	58.5	24.0
% Slope	73.0	2.0	42.8	26.2	61.2
Elevation (m)	1591.0	1472.0	1562.0	38.9	2.5
pH	7.7	7.6	7.7	0.04	0.5
		Soil nutrients			
Nitrogen (%)	0.230	0.054	0.129	0.053	41.1
Phosphorus (ppm)	17.4	7.3	12.8	3.8	29.7
Potassium (ppm)	369.7	85.2	175.5	101.9	58.1
Calcium (ppm)	6850.0	3825.0	5763.4	912.0	15.8
Magnesium (ppm)	258.0	113.3	190.1	66.5	35.0
Sodium (ppm)	356.3	21.8	96.9	120.9	124.8
Zinc (ppm)	9.7	1.1	4.2	2.6	61.9
Iron (ppm)	13.4	4.3	6.7	2.6	37.8
Manganese (ppm)	12.4	2.6	6.2	2.7	43.5
Copper (ppm)	2.7	0.6	1.3	0.6	43.0

Wasatch Mountains between American Fork Canyon on the north and the town of Santaquin on the south, a distance of 64 km. The cliffrose communities selected for study were chosen from the largest and most dense stands in the area and were thought to represent optimal habitat for the species in this part of its range.

The Wasatch Mountains are primarily composed of sedimentary limestone formations high in calcium carbonate. Rainfall in the area averages 422 mm (NOAA 1922–72), with approximately 280 mm falling between October and April (USDA 1972). The average annual temperature is 10.6 C, with frost-free period averaging 150 days (USDA 1972).

Perennial grasses, predominantly bluebunch wheatgrass (*Agropyron spicatum*), make up 65 to 85% of the original plant cover, with shrubs accounting for another 10 to 20%. The dominant shrubs in the area are: gambel oak (*Quercus gambelii*), big sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and snowberry (*Symphoricarpos oreophilus*) (USDA 1972).

METHODS

Vegetation

Ten study sites were selected from the cliffrose communities in central Utah. A 10 x 10 m study plot (0.01 ha) was established at each site. Plot boundaries were delineated using a 40-m cord with loops at each corner. Corners were secured by steel stakes. Subsampling was done using twenty 0.25m^2 quadrats placed at regular intervals within the study area. Percent cover by species (Daubenmire 1959) and by life form (Ostler et al. 1981) was estimated at each quadrat. Field data were collected during September and October 1981. Maximum annual growth for most species encountered had been reached and the annuals, though dry, were still in place.

Individual cliffrose plants as well as branches and twigs were randomly selected for sampling from each site. Average cliffrose twig length (current year's growth) on the individuals was calculated by measuring 3 twigs from 10 branches for a total of 30 measurements per study site. Leaves and current-year

TABLE 2. A comparison of average nutrient and standard deviation values for cliffrose sites in central Utah and native plant sites sampled throughout the state.

Soil nutrient factors	Cliffrose sites		Native plant sites throughout Utah*	
	$\bar{X}$	S	$\bar{X}$	S
Nitrogen (%)	0.129	0.053	0.153	0.09
Phosphorus (ppm)	12.8	3.8	42.1	43.1
Potassium (ppm)	175.5	101.9	329.0	144.1
Calcium (ppm)	5763.0	912.0	7178.0	4457.0
Magnesium (ppm)	190.1	66.5	398.8	196.4
Sodium (ppm)	96.9	102.9	—	—
Zinc (ppm)	4.2	2.6	2.1	2.3
Iron (ppm)	6.7	2.6	—	—
Manganese (ppm)	6.2	2.7	—	—
Copper (ppm)	1.3	0.6	2.1	1.4

*Data obtained from Woodward (1981).

stem growth were collected and separated for chemical tissue analysis. Tissue mineral concentrations were obtained for nitrogen, phosphorus, potassium, calcium, magnesium, zinc, manganese, iron, and copper for both leaf and stem material. Analysis of tissue was performed as described by Graham et al. (1970).

Stem cross sections were taken from five randomly selected cliffrose individuals per site to estimate stand age. The cross sections were later sanded and annual growth rings counted to determine stem age (Ferguson 1970). Stem ages were averaged to determine average stand age. Each growth ring was assumed to equal one year. Density of cliffrose was determined by counting all plants within the 0.01 ha study plot.

Degree of hedging by wildlife was categorized using nine form classes: 1 = all available, lightly hedged; 2 = all available, moderately hedged; 3 = all available, heavily hedged; 4 = largely available, lightly hedged; 5 = largely available, moderately hedged; 6 = largely available, heavily hedged; 7 = mostly unavailable; 8 = unavailable due to height; 9 = unavailable due to hedging (Anderson 1974).

Soils

Three soil samples were obtained from opposite corners and the center of each plot. Samples were taken from the top 30 cm of the soil profile. The samples were analyzed for texture (Bouyoucos 1951), organic matter (Graham 1948), pH, soluble salts, and mineral composition. Soil reaction was calculated using a glass electrode pH meter. A Beckman electrical conductivity bridge was used to determine total soluble salts. Determinations for pH and soluble salts were made on 1:1 g/v soil-water paste (Russell 1948). A buffered 1.0 neutral normal ammonium acetate solution was used to extract exchangeable calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils using DTPA (diethylene-triamine-pentaacetic acid) extracting agent (Lindsay and Norvell 1969). Ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted with sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was determined by using macro-Kjeldahl procedures (Jackson 1958).

Altitudes were obtained with an altimeter. Percent slope was measured with a clinometer. Aspect was determined with a compass. Soil penetrability was measured with a thin steel rod (0.65 cm diameter) which was pushed into the soil as far as possible by hand.

Data Analysis

Data were analyzed using means, standard deviations, coefficient of variation, and regression analyses. Tests were used to determine significant relationships between cliffrose performance and various environmental factors (Ott 1977).

All species were ranked in descending order of ubiquity using a constancy x average frequency (C x F) index, and a prevalent species list was prepared for the cliffrose community following Warner and Harper (1972). Species diversity was based on MacArthur

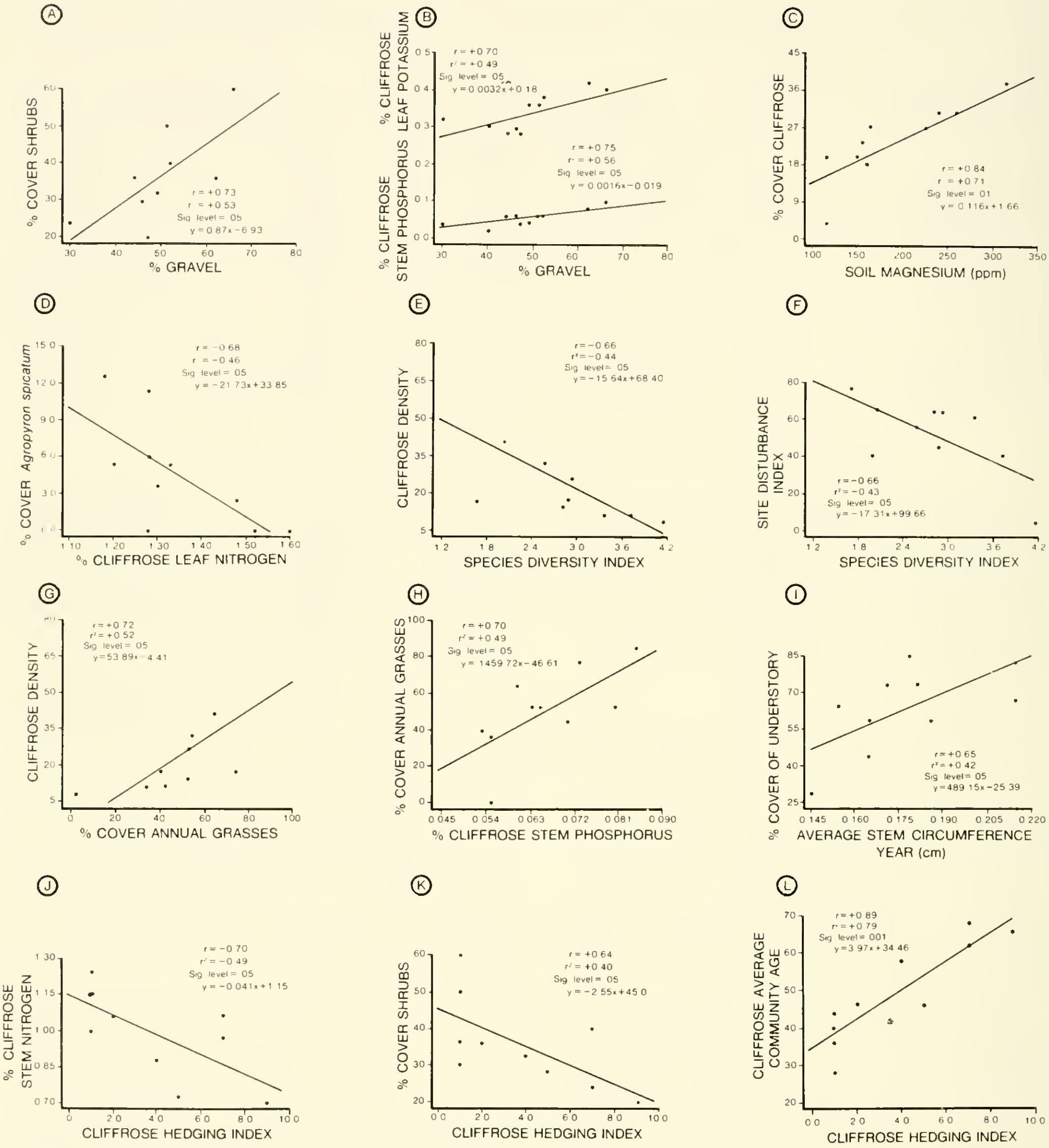

Fig. 2. Results of correlation and regression analyses with respect to site factors and vegetation parameters on the cliffrose areas: (A) the relationship between soil gravel and percent shrub cover; (B) the relationship between gravel and phosphorus and potassium in cliffrose leaf tissue; (C) the relationship between soil magnesium and cliffrose cover; (D) the relationship between cliffrose leaf nitrogen and cover of *Agropyron spicatum;* (E) the relationship between species diversity and cliffrose density; (F) the relationship between species diversity and site disturbance; (G) the relationship between annual grass cover and cliffrose density; (H) the relationship between stem phosphorus in cliffrose and annual grass cover; (I) the relationship between mean stem circumference of cliffrose and understory cover; (J) the relationship between hedging of cliffrose stems and stem nitrogen content; (K) the relationship between hedging of cliffrose stems and shrub cover; (L) the relationship between hedging of cliffrose stems and mean community age.

and Wilson's (1963) index. Plant nomenclature follows Arnow et al. (1980).

Cluster analyses (Sneath and Sokal 1973), using a dendrogram based on the cover contributions of various species at the 10 sites, were used to order the study sites.

RESULTS AND DISCUSSION

Environmental Relationships

HABITAT RELATIONSHIPS.—Cliffrose in our area generally occurred on sites with a south west exposure and an average slope of 43%.

TABLE 3. The mean, standard deviation, and coefficient of variation for nutrient ratios between cliffrose organs and soil samples. Large ratios for all nutrients, except calcium, indicate nutrient pumping has been implemented by cliffrose.

Nutrients	Leaf/soil	Stem/soil	Leaf/stem
Nitrogen	$\bar{x}$ = 12.4	$\bar{x}$ = 9.4	$\bar{x}$ = 1.39
	S = 5.8	S = 5.1	S = .28
	CV = 47.8	CV = 54.3	CV = 20.1
Phosphorus	$\bar{x}$ = 55.9	$\bar{x}$ = 46.3	$\bar{x}$ = 1.31
	S = 19.2	S = 17.2	S = .50
	CV = 40.2	CV = 49.3	CV = 38.2
Potassium	$\bar{x}$ = 24.1	$\bar{x}$ = 22.3	$\bar{x}$ = 1.16
	S = 9.7	S = 11.0	S = .25
	CV = 40.2	CV = 49.3	CV = 21.6
Calcium	$\bar{x}$ = 2.7	$\bar{x}$ = 2.3	$\bar{x}$ = 1.12
	S = .6	S = .62	S = .19
	CV = 22.2	CV = 27.0	CV = 17.0
Magnesium	$\bar{x}$ = 18.2	$\bar{x}$ = 10.0	$\bar{x}$ = 1.77
	S = 10.8	S = 4.1	S = .34
	CV = 59.3	CV = 41.0	CV = 19.2
Zinc	$\bar{x}$ = 126.5	$\bar{x}$ = 80.3	$\bar{x}$ = 1.65
	S = 52.8	S = 33.8	S = .60
	CV = 41.7	CV = 42.1	CV = 36.4
Manganese	$\bar{x}$ = 8.4	$\bar{x}$ = 5.0	$\bar{x}$ = 1.71
	S = 4.7	S = 2.7	S = .37
	CV = 56.0	CV = 38.5	CV = 21.6
Copper	$\bar{x}$ = 6.9	$\bar{x}$ = 7.8	$\bar{x}$ = .88
	S = 2.8	S = 3.0	S = .09
	CV = 40.6	CV = 38.5	CV = 10.2

TABLE 4. A prevalent species list for the study sites. Species are ranked by importance based on the C x F index. Letters in parentheses designate the species life-form class and origin: P = perennial; A = annual; S = shrub; F = forb; G = grass; N = native; and I = introduced.

Species	Percent constancy	Average frequency	C x F index	Percent average cover
1. *Bromus tectorum* (AGI)	100	90.0	9000	36.9
2. *Cowania mexicana* (PSW)	100	64.0	6400	23.7
3. *Alyssum alyssoides* (AFI)	90	40.0	3600	3.5
4. *Agropyron spicatum* (PGM)	80	35.6	2850	4.6
5. *Poa secunda* (PGM)	40	31.3	1252	1.4
6. *Bromus japonicus* (AGI)	30	35.0	1050	0.9
7. *Linaria dalmatica* (PFI)	10	75.0	750	1.0
8. *Chrysothamnus nauseosus* (PSN)	60	10.8	650	1.2
9. *Sisymbrium altissimum* (AFI)	50	12.0	600	0.2
10. *Sporobolus cryptandrus* (PGM)	20	17.5	350	0.2
11. *Erodium cicutarium* (AFI)	10	35.0	350	0.0
12. *Artemisia ludoviciana* (PFR)	40	7.5	300	0.3
13. *Artemisia tridentata* (PSN)	60	4.2	250	0.7

Elevation varied little across the sites and averaged 1,562 m (Table 1). The communities were located along the gravelly shoreline of ancient Lake Bonneville, which covered much of the western half of Utah approximately 12,000 years ago (Bissell 1968). Seven of the sites had gravelly sandy loam soils, two occurred on gravelly loams, and one on a gravelly clay loam. Soils on the sites were heavily skeletal (48.7% gravel by weight), had an av-

TABLE 5. A comparison of the mean, standard deviation, and coefficients of variation for mineral content in cliffrose stems and leaves. A paired t-test was used to determine significant nutrient differences between organs.

Cliffrose nutrient*	Stems			Leaves			Paired t-test significance level
	$\bar{X}$	S	CV	$\bar{X}$	S	CV	
Nitrogen (%)	1.00	0.20	20.0	1.40	0.10	7.1	.001
Phosphorus (ppm)	0.06	0.02	33.3	0.07	0.01	14.3	NS
Potassium (ppm)	0.30	0.07	23.3	0.34	0.05	14.7	.05
Calcium (ppm)	1.30	0.27	20.8	1.40	0.16	11.4	.05
Magnesium (ppm)	0.17	0.04	23.5	0.30	0.90	30.0	.001
Zinc (ppm)	22.90	6.30	27.5	22.70	5.30	23.3	NS
Iron (ppm)	488.40	156.00	31.9	763.70	229.00	30.0	.01
Manganese (ppm)	25.70	4.60	17.9	43.60	10.50	24.1	.001
Copper (ppm)	9.00	1.50	16.7	7.80	0.75	9.6	.01

TABLE 6. An interregional comparison of plant nutrient concentrations for cliffrose in central Utah, cliffrose in Arizona, and the average of 11 rosaceous plants sampled in Wisconsin.

	N	P	K	Ca	Mg	Fe	Mn	Zn	Cu
			(%)					(ppm)	
Cliffrose (central Utah)									
Leaves	1.4	0.07	0.34	1.4	0.30	764	44	23	8
Stems	1.0	0.06	0.30	1.3	0.17	488	26	23	9
Cliffrose (northern Arizona)	1.0	0.06	0.34	1.0	0.12	76	9	19	7
Rose family (Wisconsin)**	1.5	0.28	1.50	1.0	0.48	154	375	44	5
	N	P	K	Ca	Mg	Fe	Mn	Zn	Cu
			(%)					(ppm)	
Soil nutrients									
(central Utah)	0.13	13	176	5763	190	7	6	4	1.32
(northeast Arizona)*	0.07	11	116	2358	639	5	4	2	0.46

*Data from Fairchild and Brotherson (1980).
**Data from Gerloff et al. (1964).

erage penetrability of 17.9 cm, and showed an average texture of gravelly sandy loam. Adjacent finer-textured soils of the old lake bottom apparently create a barrier to many shrubs, including cliffrose, confining them to the well-drained, lighter-textured soils of the foothills.

Soil reaction was constant across all sites with the pH being slightly basic (7.7). Cline (1960) showed cliffrose to tolerate pH's ranging from 6.8 to 8.7. Soluble salts were low, ranging from 330 ppm to 477 ppm with a mean of 389 ppm (Table 1).

Average soil nutrient concentrations in sieved samples are also given in Table 1. Data show sodium concentrations to be the most variable among sites, with calcium being the least variable. Calcium was the most abundant essential element in the sampled and nitrogen the least abundant. Our sites were generally lower in all nutrients sampled (except for the micronutrient zinc) than a broad spectrum of range soils reported by Woodward et al. (1984) (Table 2). Because nutrient deficiencies in soils are difficult to document without controlled laboratory conditions, it is important to understand with respect to our cliffrose sites that soil skeletal material reduces the volume of available nutrient or water per unit depth of profile (Crowther and Harper 1965). This is because both the nutrient and water content of soils are often determined from sieved samples in which particles over 2 mm diameter are removed. Because our soils were so heavily skeletal, nutritional deficiencies on the cliffrose sites may be even more extreme than our data portray.

Infiltration rates and depths of percolation of water are highly correlated with soil texture (Croft and Bailey 1964). Gravelly soils allow water to percolate to depths which may only be available to deep-rooted plants. Water percolation may also leach nutrients to deeper layers. Correlation analysis revealed significant positive relationships ($p < 0.01$) between shrub cover (primarily cliffrose), stem phosphorus, and leaf potassium concentrations in cliffrose and percent gravel in the soil (Figs. 2A and 2B). Cline (1960) reports that most lateral branching in the roots of bitterbrush and cliffrose was within the top 30 cm, but when lateral branching occurred at deeper regions in the soil profile, it was extensive and appeared to correlate with increased availability of moisture and nutrients. The average rooting depth of cheatgrass, our major understory species, has been reported by Klemmedson and Smith (1965) to be 30 cm. Cline (1960), on the other hand, reported cliffrose rooting depth to average 120 cm, with the deepest depths reported at 300 cm. These differences may help to explain the positive relationships between mineral concetrations in cliffrose tissue and percent gravel in the soil. The greater the gravel content, the deeper the leaching and the greater the opportunity for the deep roots of cliffrose to come in contact with and absorb them. Because of the differences in rooting depth, and the fact that the period of most active moisture absorption for cheatgrass is in late fall and early spring (Klemmedson and Smith 1964), a time when moisture in deeper soil profile levels is usually abundant, we feel competition for moisture between adult cliffrose individuals and cheatgrass may be less severe than one might otherwise predict. Competition for available nutrients may also be less than one would normally anticipate.

MINERAL NUTRIENT RELATIONSHIPS.—Due to the general absence of soil moisture and low levels of soil nutrient concentrations which are characteristic of cliffrose-dominated sites, cliffrose appears to have evolved strategies enabling it as a species to tolerate infertile environmental conditions. Cliffrose is evergreen and therefore can immediately begin to photosynthesize as soon as winter breaks. The plant flowers in spring, when soils are recharged with moisture and organic matter has been broken down releasing available nutrients to the soil. Also, since cliffrose is evergreen, its nutrient demands should be much less than for other plants that must reconstruct their foliage each year. Conservation of nutrients and the exploitation of resources during peak supply would favor the survival of cliffrose on pioneer sites (Harper and Buchanan 1982). Deep taproots, with regions of increased lateral branching, would also aid in survival during dry periods. Cliffrose may experience success on sites that are low in nitrogen because of its ability to fix nitrogen (Righetti and Munns 1980, Nelson 1983, Righetti et al. 1986).

The insolubility of iron in the alkaline soils of western United States often renders the element unavailable to plants (Mortvedt et al. 1972). Low concentrations of iron were recorded on several of our sites (Table 1). The ratio between iron in cliffrose leaves and the soil where it grows (Table 3) was 127. Ratios for all nutrients, except calcium, were relatively high, especially for the macronutrients (Table 3). This demonstrates that cliffrose, like other shrubs (Brotherson and Osayande 1980), has the ability to actively pump nutrients. This ability may also help explain how the plant is able to exist on sites that are somewhat nutrient deficient.

Positive correlations ($p \leq 0.05$) developed between percent cover of shrubs (predominantly cliffrose) and concentrations of stem phosphorus, stem nitrogen, stem copper, and leaf potassium in cliffrose which would indicate that where shrub cover is high, cliffrose does its best job of pumping nutrients. Cover of associated understory species also increased as soil nutrient concentrations increased. Cliffrose cover itself was found to be positively correlated ($p < 0.01$) with soil magnesium (Fig. 2C), yet parent material for the gravels of the cliffrose sites studied was calcium carbonate ($CaCO_3$). Dolomite ($CaCO_3$-$MgCO_3$) is relatively scarce in the areas near our study sites, and parent material for the Wasatch Mountains in central Utah is generally low in magnesium. So, local weathering patterns that free magnesium ions into the soil profile may be important to cliffrose ecology. For example, Brotherson et al. (1985) showed the distribution of plant communities to be strongly related to localized weathering patterns. Further, plant communities surrounding Utah Lake in central Utah show exchangeable magnesium concentrations ranging from 247 to 1,039 ppm (Brotherson and Evenson 1981). Brotherson and Evenson's (1981) data show magnesium to become progressively more concentrated in the more highly weathered soils as one moves from the mountain foothills to the valley floor, and finally to the lake's edge.

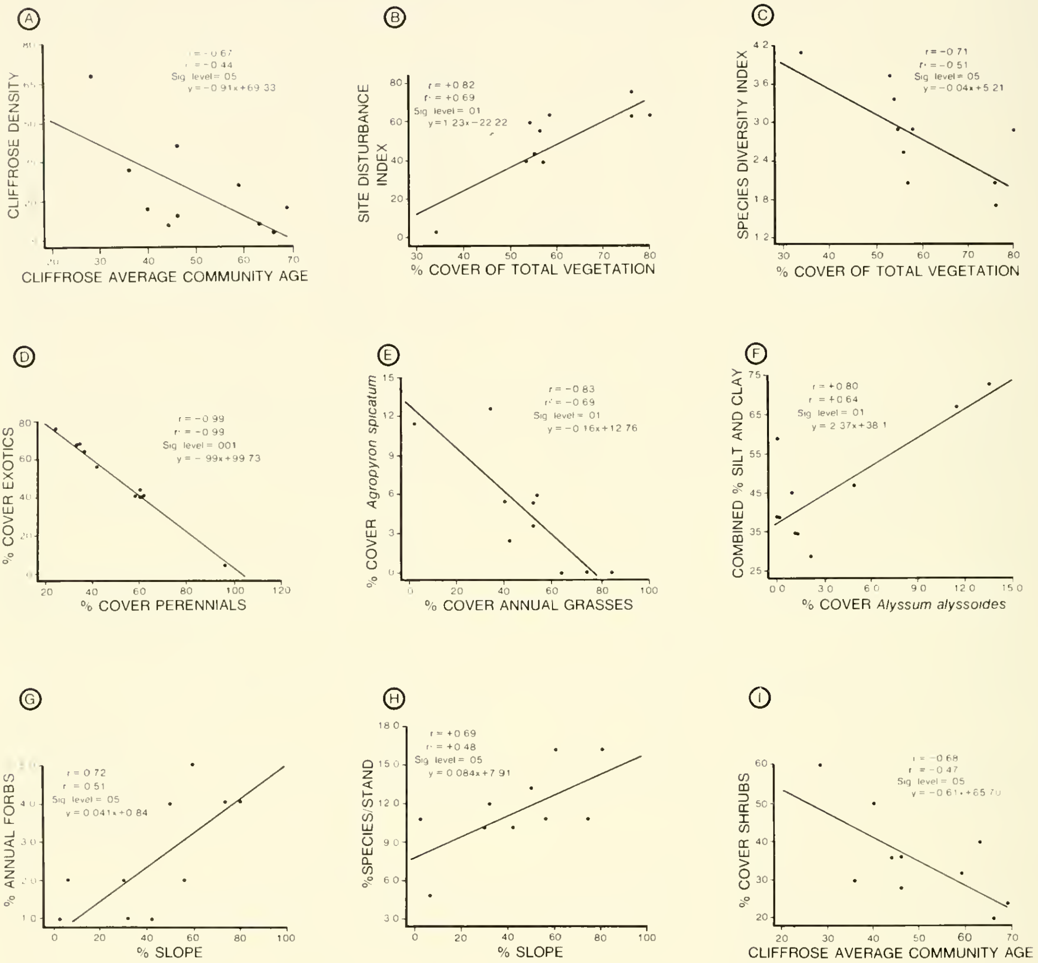

Fig. 3. Results of correlation and regression analyses with respect to site factors and vegetation parameters on the cliffrose areas: (A) the relationship between average community age and cliffrose density; (B) the relationship between cover of total vegetation and site disturbance; (C) the relationship between cover of total vegetation and species diversity; (D) the relationship between perennial cover and exotic cover; (E) the relationship between annual grass cover and cover of *Agropyron spicatum;* (F) the relationship between cover of *Alyssum alyssoides* and soil silt and clay; (G) the relationship between percent slope and number of annual forbs/stand; (H) the relationship between percent slope and number of species/stand; (I) the relationship between mean community age and shrub cover.

The cliffrose sites were dominated in the understory by exotic annuals (Table 4), all of which exploit site moisture and nutrient reserves at a time of peak availability. These exotics sprout, use up much of the moisture and nutrient reserves, produce seed, and die by the time other plants are emerging from dormancy. Since these exotic annuals are such successful competitors, this could only happen if the overstory and the understory were exploiting different nutrient levels in the soil.

Correlation analysis indicated that as the percent cover of bluebunch wheatgrass increased, nitrogen concentrations in cliffrose leaves decreased ($p \leq 0.05$) (Fig. 2D). Also, cliffrose density was negatively correlated ($p \leq 0.05$) with species diversity (Fig. 2E), and species diversity was negatively correlated with site disturbance (Fig. 2F). Further, as cliffrose density increased, percent cover of annual grasses increased ($p \leq 0.05$) (Fig. 2G); and, concurrently, concentrations of phos-

TABLE 7. Measurements concerning cliffrose population density, plant age, community age, and plant anatomy.

Soil nutrient factors*	High	Low	Mean	Standard deviation	Coefficient of variation
Density (plants/ha)	6700.0	700.0	2450.5	1851.0	75.5
Average height (cm)	240.0	103.0	171.8	39.4	22.9
Average community age	68.6	28.3	49.5	13.6	27.5
Individual plant age	162.5	11.1	48.6	28.7	59.1
Average twig length (cm)	13.3	2.0	6.3	3.4	54.0

phorus in cliffrose stems increased ($p \leq 0.05$) (Fig. 2H). Understory cover (predominantly annual grasses) and average increase in circumference per year of cliffrose stems were also positively correlated ($p \leq 0.05$) (Fig. 2I). These facts tend to indicate a greater competition between cliffrose and deep-rooted perennial grasses for moisture and nutrients than between cliffrose and the more shallow-rooted annual grasses.

CLIFFROSE TISSUE CHEMISTRY.—The current annual growth of cliffrose stems and leaves was chemically analyzed for mineral nutrient content. Table 8 compares average nutrient values obtained for cliffrose stems and leaves. Tests for significant differences between stem and leaf nutrients were made using a paired t-test (Ott 1977). Significantly higher concentrations ($p < 0.05$) of minerals were found in cliffrose leaves than in cliffrose stems for all nutrients analyzed, with the exception of copper, phosphorus, and zinc. Copper concentrations were significantly lower in the leaves, whereas phosphorus and zinc showed no differences. The stem nutrient showing the least variability between sites was copper, while iron showed the most variability. Nitrogen concentration in the leaf was least variable, while iron and magnesium were the most variable leaf nutrients. High concentrations of iron were found in both leaves and stems of cliffrose (Table 5). Leaf samples were recollected from all the sites and reanalyzed to check against possible sample contamination. The samples were washed in distilled water, oven dried, and hand ground with a ceramic mortal and pestle. Results of the second analysis confirmed the accuracy of the first.

Nutrient values obtained for cliffrose in central Utah were compared with values for the species at other geographical locations (Fairchild and Brotherson 1980). Also, the values of this study were compared with analyses for other species of the rose family (Gerloff et al. 1964) (Table 6). The differences between cliffrose nutrient content in central Utah and those in northeastern Arizona are generally small and may be attributed to differences in the soil nutrient pool. Unfortunately, soil data for the Wisconsin study were not available. In comparing cliffrose chemistry in central Utah with that in northeastern Arizona and with other members of Rosaceae from Wisconsin, one notes tissue iron concentrations to be highest in cliffrose from central Utah. Soil samples for the Utah and Arizona studies are relatively low in available iron. At present, the high iron concentrations in cliffrose from central Utah remain unexplained. One will also note that average tissue manganese for rosaceous species from Wisconsin is much greater than values for either of the cliffrose studies. Soils in the eastern United States are generally acidic, which would make more manganese available for passive absorption. In the West, soils are generally alkaline, which keeps manganese relatively insoluble and unavailable for plant use. Hoffer (1941) points out that nitrogen fixation and ammonification processes are dependent on manganese; therefore, soils high in calcium carbonate are generally deficient in this element. The high differences in manganese concentrations between eastern and western United States plants are most likely due to availability in the soil. With the exception of calcium, macronutrient concentrations for cliffrose sites from both Utah and Arizona were lower than average concentrations found for rosaceous members in Wisconsin (Table 9). The parent material for the soils of cliffrose in central Utah and northeastern Arizona are high in calcium. Further research is needed to determine to what extent varying nutrient concentrations between different species can be attributed to natural selection as opposed to inaccurate sampling and analyzing techniques.

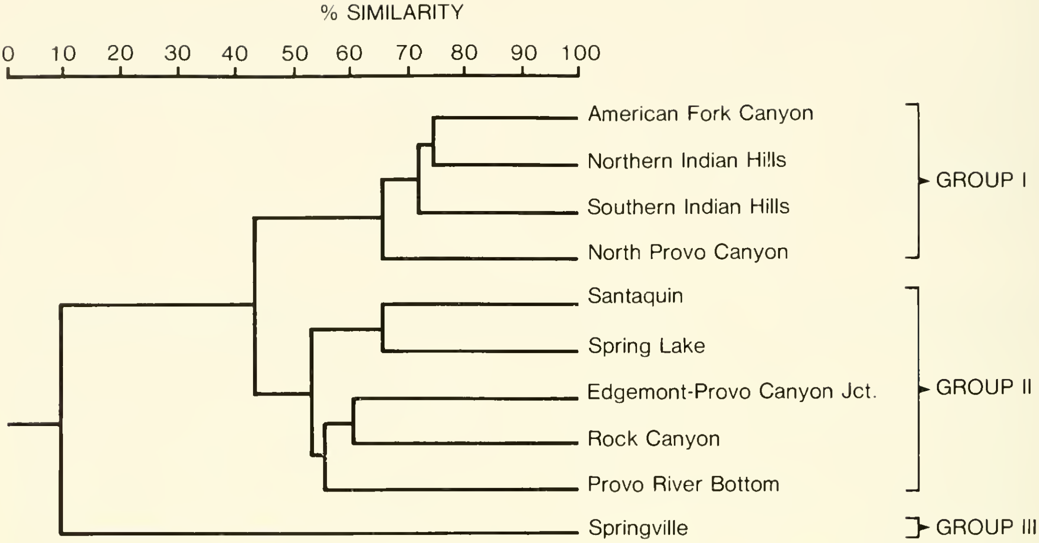

Fig. 4. A dendrogram showing cluster groups between study sites based on percent similarity of species cover by stand.

Animal Utilization.—Degree of hedging by wildlife showed a negative correlation ($p \leq 0.05$) with percent nitrogen found in the stems of cliffrose (Fig. 2J). This is best explained by the differential stem growth stimulated by varying degrees of plant pruning due to utilization. The greater the stem elongation, the more dilute stem nitrogen should become. Data also indicated that the older cliffrose communities were more heavily hedged than the younger communities.

Cliffrose utilization increased as percent cover of shrubs on the sites decreased ($p \leq 0.05$) (Fig. 2K). Also, utilization increased as community age of the cliffrose stands increased ($p \leq 0.05$) (Fig. 2L); and as the age of the cliffrose stands increased, cliffrose density decreased ($p \leq 0.05$) (Fig. 3A). Density measurements revealed central Utah cliffrose communities to have an average of 2,451 plants per hectare (Table 7). The average height of cliffrose on our study sites was 171.8 cm, with the shortest community averaging 103 cm and the tallest 240 cm (Table 7). Increases in utilization of the older cliffrose stands can most likely be attributed to older communities having fewer plants, which would tend to increase the grazing pressure per plant. Further, the large plants should provide better thermal cover, as well as better escape cover, thus providing incentive for animals to concentrate in their vicinity with resultant higher use.

Community Relationships

Community Structure.—A percent similarity index between communities was calculated using data based on measurements of cover. Cluster analysis was then used to group the cliffrose stands.

The cluster based on cover of individual species showed the sites to have an average percent similarity of 42.8% (Fig. 4). The dendrogram (Fig. 4) shows three relatively distinct groups. Cover data for stands in Group I, Group II, and Group III were averaged (Table 8). Group I had the greatest cover and was dominated by exotic annuals, mainly cheatgrass. Group II had the next greatest cover and was also dominated by annuals, but less so than in Group I. Percent perennial cover in Group II was slightly higher than in Group I, but cliffrose cover remained constant. Data showed the major life form for Group III to be perennial grasses. Unlike the other cliffrose study sites, this stand recorded few annuals during our original investigation. However, when reexamined in the spring (1982), spots originally recorded as bare ground were found to be heavily covered by the small introduced annual, jagged chickweed (*Holosteum umbel-*

TABLE 8. Cliffrose study sites as grouped by cluster analysis. Sites are grouped based on percent similarity of the averaged percent cover contributed by prevalent species. Figure 3 shows American Fork Canyon–Northern Provo Canyon in Group I, Santaquin–Provo River Bottom in Group II, and Springville in Group III. Letters in parentheses designate the species life-form class and origin: P = perennial; A = annual; S = shrub; F = forb; G = grass; N = native; and I = introduced.

Species	Group I	Group II	Group III
1. *Bromus tectorum* (AGI)	61.0	25.0	0.4
2. *Cowania mexicana* (PSW)	26.0	26.0	3.5
3. *Alyssum alyssoides* (AFI)	7.0	1.2	0.3
4. *Agropyron spicatum* (PGM)	2.3	5.1	11.5
5. *Poa secunda* (PGM)	0.3	0.1	10.5
6. *Bromus japonicus* (AGI)	0.2	1.6	0.0
7. *Linaria dalmatica* (PFI)	0.0	2.1	0.0
8. *Chrysothamnus nauseosus* (PSN)	3.1	0.0	0.0
9. *Sisymbrium altissimum* (AFI)	0.5	0.4	0.0
10. *Sporobolus cryptandrus* (PGM)	0.0	0.1	0.0
11. *Erodium cicutarium* (AFI)	0.1	0.0	0.0
12. *Artemisia ludoviciana* (PFR)	0.1	0.0	2.3
13. *Artemisia tridentata* (PSN)	1.0	0.1	3.1
Total cover	102.1	61.7	32.1

latum). According to Arnow et al. (1980), the plant grows on highly disturbed sites. Jagged chickweed was not found established to any degree of significance on any of the other sites following reexamination. In spite of this addition, Group III was distinctly different from the other groups in terms of plant cover composition. Total cover values and species composition showed major differences among the three groups (Table 8).

DIVERSITY.—Diversity has two conceptual aspects that deserve attention: (1) the number of species per unit area and (2) the evenness of abundance among the species present. Community diversity (MacArthur and Wilson 1963) on our sites varies from a high of 4.1 to a low of 1.7, with a mean of 2.8 (Table 9). The low figure was correlated with the highest incidence of cheatgrass on a site and indicates that only a few species were contributors to the vegetative composition. The high figure was associated with a site which had little cheatgrass cover and where several species were shown to contribute to the vegetative cover.

Assuming the cover contributed by exotics to be highly correlated with the degree of site disturbance (Klemmedson and Smith 1964), we formulated a disturbance index based on the amount of cover contributed by introduced species on our sites. Correlation analysis showed a positive relationship ($p \leq 0.01$) between the site disturbance index and percent cover of total vegetation (Fig. 3B). Further, a negative correlation ($p \leq 0.05$) was found between species diversity and total plant cover (Fig. 3C). As the site disturbance index increased, species diversity decreased (Fig. 2F). It appears, therefore, that site disturbance has tended to promote low diversity in the vegetation on our sites by allowing introduced annuals to invade into open areas where they complete their growth in the early spring while soil moisture is still abundant. The increased competition from the introduced exotics would have a crowding effect on other species and thus lead to an eventual decrease in diversity.

The prevalent species for the cliffrose sites in central Utah are listed in descending order based on the C x F index (Table 4). Again, the importance of exotics on our sites is illustrated. Cheatgrass (*Bromus tectorum*) is the most common species on the list, followed by cliffrose and madwort (*Alyssum alyssoides*), an introduced annual from Europe (Arnow et al. 1980). Nearly half the species on the list (6 out of 13) are introduced exotics (Table 4), all of which are extremely successful on disturbed sites. The data showed an average of 7.6 perennials and 3.9 annuals per stand, yet annuals contributed almost half the total cover (Table 9). Significant negative correlation ($p \leq 0.01$) also occurred between cover of perennials and cover of exotics (Fig. 3D), suggesting that perennials must decline before invading exotics can become abundant. The correlation between cover of annual grasses and the

TABLE 9. Highs, lows, means, standard deviations, and coefficients of variation for various biotic factors and life-form classes associated with the cliffrose sites in central Utah.

Factors	High	Low	Mean	Standard deviation	Coefficient of variation
% Total vegetative cover	80.0	33.8	59.7	13.9	23.3
% Exposed rock	34.1	3.1	20.1	9.7	48.3
% Bare ground	12.8	0.0	5.8	5.0	86.2
% Litter	26.4	6.6	14.8	6.4	43.2
% Mosses	13.4	0.0	3.1	4.9	158.1
% Lichens	4.1	0.0	1.3	1.4	107.7
% Trees	1.1	0.0	0.2	0.4	200.2
% Shrubs	60.3	20.2	35.4	12.2	34.5
% Perennial forbs	17.7	0.0	3.2	6.1	190.6
% Annual forbs	14.0	0.0	4.4	4.9	111.4
% Perennial grasses	65.9	0.0	11.9	19.8	166.4
% Annual grasses	74.4	1.1	45.1	19.7	43.7
% Perennials	96.6	23.5	50.5	20.9	41.4
% Annuals	76.5	3.4	49.5	20.9	42.2
% Exotics	76.1	3.4	51.1	20.7	40.5
# Perennials/study site	11.0	2.0	7.6	2.5	32.9
# Annuals/study site	7.0	2.0	3.9	1.6	41.0
# Shrubs/study site	6.0	2.0	3.8	1.3	34.2
# Species/study site	16.0	5.0	11.5	3.2	27.8
Species diversity index*	4.1	1.7	2.8	0.8	28.6

*MacArthur-Wilson (1963) diversity index.

perennial bluebunch wheatgrass (*Agropyron spicatum*) was also negative ($p \leq 0.01$) (Fig. 3E).

The distribution on our sites of the annual forb madwort is positively correlated ($p \leq 0.01$) with percent silt and percent clay in the soil (Fig. 3F). This relationship can most likely be attributed to the moisture and nutrient factors associated with finer-textured soils. The number of annual forbs on a site generally increased as the slope steepness increased ($p \leq 0.05$) (Fig. 3G). Also, the number of species per study site increased as slope steepness increased ($p \leq 0.05$) (Fig. 3H). This would indicate that the sites on the steeper slopes have more microhabitats and are probably less disturbed. The correlations may also be related to the reluctance of domestic grazing animals, the major disturbing influence of the past on these sites, to make use of the steeper slopes.

LIFE FORMS.—Cliffrose sites typically show environmentally stressed conditions related to such things as extremes in moisture, temperature, and soil nutrients. Plants that are successful on the sites are generally able to withstand a broad range of environmental fluctuations, or, as in the case of annuals, they complete their life cycles during hospitable times of the year. Of the total cover that averaged 59.7%, annual grasses contributed the largest part with 45.1%, shrubs furnished 35.4%, perennial grasses contributed 11.9%, annual forbs accounted for 4.4%, and perennial forbs contributed only 3.2% (Table 9). Gambel oak (*Quercus gambelii*) was the only tree found on the sites, and it played an insignificant role in the vegetation. Perennials contributed 50.5% of the total cover, while annuals contributed 49.5%. Averaging the constancy x frequency (C x F) index values of Table 4, we found annual grasses to be twice as important in the community as shrubs (Table 10). The C x F index reflects the uniformity with which individuals of a species are distributed across the site sampled rather than the amount of biomass produced. The values show annual forbs to be slightly more important than perennial forbs or perennial grasses in the community. Annuals (Table 10) were shown to have a higher prominence in the community than perennials.

CLIFFROSE AGE AND COMMUNITY STRUCTURE.—Cliffrose plants of varying basal circumferences were aged. Linear regression was used to establish an age-circumference relationship (Fig. 5). This relationship had an r^2 value of $+0.73$ and was significant at $p \leq 0.001$. The prediction equation for the relationships is $Y = 4.73$ (basal circumference) $+ 5.45$. The average variation about the y-axis is ±6.7 years.

Table 10. Life forms listed in order of importance to the vegetative composition. Values were obtained by averaging the product of percent species constancy between sites and percent species frequency within sites for species of each life-form class.

Life forms	Constancy x frequency index
Annual grasses	5025
Shrubs	2433
Annual forbs	1517
Perennial grasses	1483
Perennial forbs	525
Total annuals	6542
Total perennials	4441

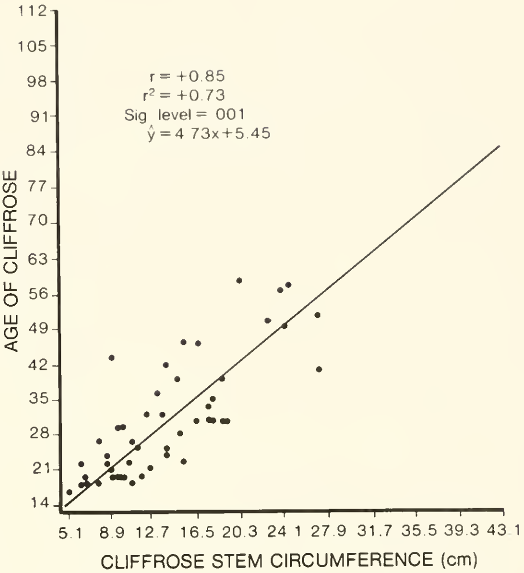

Fig. 5. The relationship between the circumference (cm) of cliffrose stems and the number of annual growth rings counted (age) of 50 cliffrose plants sampled.

Basal circumference measurements (30 per site) were randomly obtained for 9 of the 10 communities. The Springville community had only 18 living cliffrose plants. From these basal measurements, the plants of each stand were aged. By combining the estimated ages of the 288 plants studied, we constructed a histogram to show the general age distribution of cliffrose in central Utah (Fig. 6). The x-axis of the histogram shows the age classes (in 5-year intervals) and the year corresponding with the period of establishment for the age class. The y-axis is the number of plants found within each age class. The histogram shows the median cliffrose age to be between 25 and 30 years. The youngest plant found in any of the communities was 11 years, the oldest was 163 years, and the average age was 48.6 years (Table 7). The youngest average community age was 28.3 years, the oldest 68.6, and the mean was 49.5 years (Table 7).

Cliffrose Establishment.—The histogram indicates that since about 1957 there has been a steady decline in the establishment of cliffrose in central Utah. The graph also shows a substantial decline in numbers of new plants between the years 1942 and 1947. Correlation analysis showed the percent cover by shrubs (predominantly cliffrose) decreased as the average community age of cliffrose increased ($p \leq 0.05$) (Fig. 31). The older cliffrose stands do not appear to be replacing themselves with younger plants (Figs. 3A and 6).

Reasons for establishment failure most likely represent a combination of factors. Some possible explanations should include: (1) cliffrose is cyclic in its establishment, (2) seed predation by rodents may be high, (3) plant diseases may be eliminating seedlings, (4) insects and/or small mammals may destroy seedlings, (5) climate may currently be unfavorable, (6) intraspecific competition between age classes may be extreme, (7) interspecific competition, (8) establishment requires trampling and utilization of the sites by livestock and wildlife, and (9) reproduction may be destroyed by fire.

Concern that small seedlings were overlooked during the initial data collecting period led us to reexamine all of the sites to confirm original findings. No seedlings were discovered at this time. Neither were seedlings found in any of the 200 0.25 m^2 quadrats used to estimate plant cover.

Cyclic Establishment: According to Alexander et al. (1974), cliffrose produces a good seed crop every 2 years, and young plants begin bearing seed as early as 5 years. Figure 7 is a graph comparing annual rainfall patterns with the number of cliffrose plants established each year during a 50-year period (1922–1972). Precipitation data were smoothed out using a 10-year running average to eliminate the visual impact of extremely high or low years and to emphasize long-term trends (Croft and Bailey 1964). In comparing precipitation and establishment trends, it appears that increases in rainfall may reduce cliffrose seedling success. The observed decline in

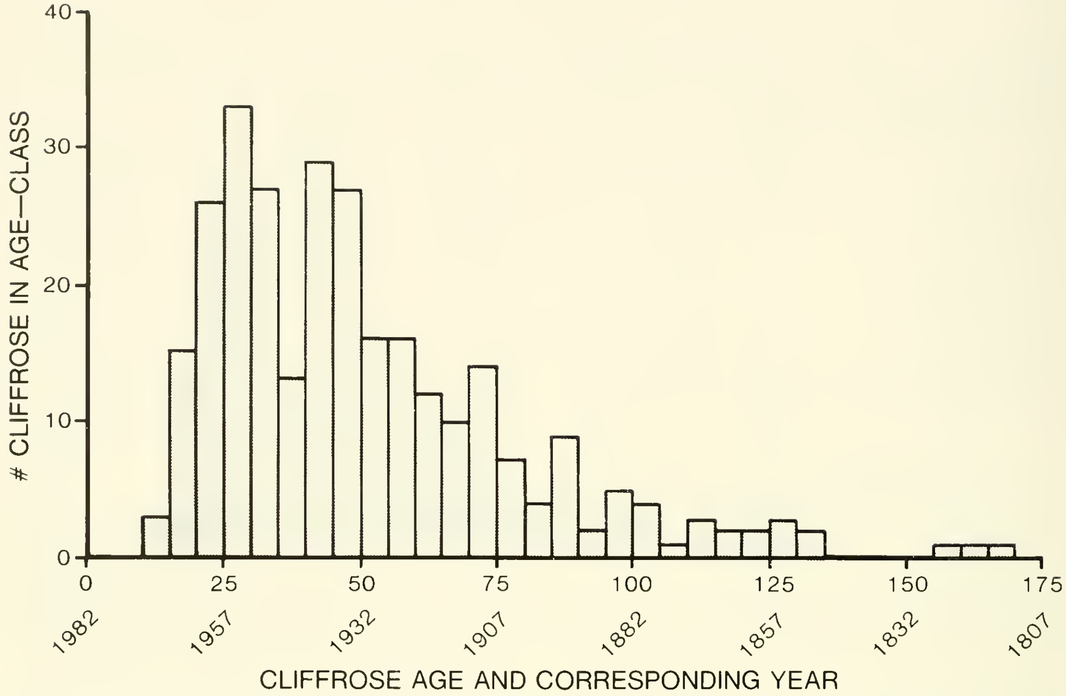

Fig. 6. A histogram depicting the establishment success and trend of cliffrose over the last 175 years.

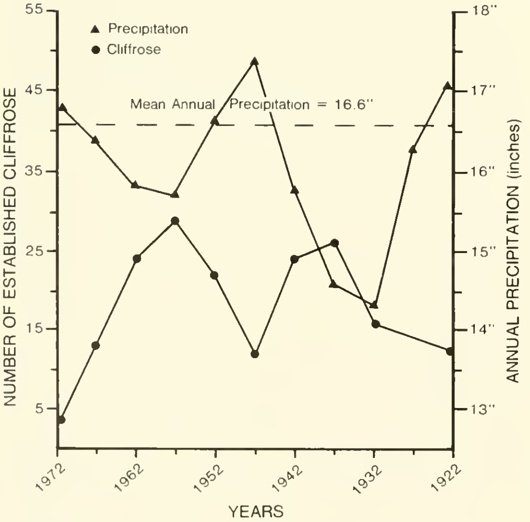

Fig. 7. A graph depicting the relationship between precipitation trends and cliffrose establishment success and trend over a 50-year period.

plants established between the years 1942 and 1947 (Fig. 6) was a peak rainfall period for the area considered. Comparison of the last 25 years for precipitation per year versus cliffrose establishment suggests that diminishing seedling success may be somewhat related to cyclic rainfall patterns.

Predation: Seed and seedling predation by rodents is a subject addressed in several papers. Alexander et al. (1974) note that clusters of new cliffrose seedlings are quite common due to rodent caches. Young and Evans (1981) state that if caches are not found by rodents, the seedlings will die from intraspecific competition. They also point out that the rodent will often miss a seedling or two, which allows for plant establishment. Seed predation by rodents may in reality enhance species dispersal and establishment.

Disease: Lack of knowledge concerning diseases of cliffrose dictates that little be said concerning this subject. No papers addressing the topic were found in the literature. However, an exceptionally high rate of mortality has been noted for greenhouse-grown seedlings of both cliffrose and bitterbrush due to damping-off fungi. Though damping-off is common among greenhouse stock, bitterbrush and, even more so, cliffrose seemed to be especially susceptible to such diseases (B. L. Welch, personal communication). Cliffrose susceptibility to damping-off under natural conditions is not known. This could be an explanation for the apparent inverse relationship found between cliffrose establishment and average annual precipitation.

Insects: The impact of insects and their relationship with cliffrose is also not well known. Again the literature revealed no studies on the subject. Although little is known concerning the subject, insect predation should not be completely ruled out as a possible influencing factor.

Climate: Drought, as a possible explanation for the lack of seedling establishment in cliffrose since 1957, is not a good choice. Over the centuries, cliffrose has adapted to an environment which is, at times, extremely dry. Climatology records (NOAA 1922–1972) show that during the major periods of decreasing seedling establishment, average precipitation was above the normal amounts recorded for preceding years.

Competition: Intraspecific competition probably has little to do with the downward trend in recent years. It is difficult to imagine that a species which has been successfully established for hundreds of years would suddenly begin outcompeting itself into possible local extinction.

However, numerous studies have been published (interspecific competition) dealing with the extreme competitiveness demonstrated by exotic annuals (Stewart and Hull 1949, Piemeisel 1951, Holmgren 1956, Klemmedson and Smith 1964, Young et al. 1972, Giunta et al. 1975, Mack 1981, Mack and Pyke 1983), particularly cheatgrass.

Cheatgrass invasion into Utah is fairly recent, having been introduced around the turn of the century (Klemmedson and Smith 1964). Studies show that cheatgrass successfully outcompetes weeds and perennial grasses which are slow growing or spring germinating (Piemeisel 1951, Stewart and Hull 1949). Evans et al. (1967) state that cheatgrass consistently closes stands to the establishment of perennial grass seedlings. Warg (1938) and Hulbert (1955) obtained success for cheatgrass germinations (under optimum conditions) as high as 99.5%. The density obtained by cheatgrass can vary greatly, depending on the conditions. Stewart and Hull (1949) found cheatgrass to vary from 1,080 to 15,000 seedlings per m^2. This gives an idea of the potential competition for moisture that cheatgrass can exert if conditions are favorable.

Studies by Giunta et al. (1975) showed that in cheatgrass stands success in the germination and establishment of cliffrose was increased as width of soil scalps increased. They also showed the average number of cliffrose plants surviving after five years in a 100-linear-foot row to be 5, 13, 19, and 59 with scalp widths of 4, 8, 16, and 24 inches, respectively. Holmgren (1956) worked with bitterbrush. He stated that high mortality occurred in the better seedling stands during the first year or so after germination. Holmgren (1956) also states that moisture at the time of germination and during the initial growth period is probably the most crucial factor associated with bitterbrush seedling success. Holmgren's (1956) study shows bitterbrush germination rates for study plots that were cleared of all competition to be 90%, with 66% surviving after the first year. Plots in which only broadleaf weeds were allowed had a 91% germination, with 48% surviving the first year. Where only cheatgrass was allowed, germination was 46%, with 0% surviving after only three months. Holmgren (1956) then concludes, "In cheatgrass stands, few bitterbrush seedlings are able to survive the first summer. The competitive effect of cheatgrass generally becomes manifest early in the growing season, coinciding with its period of rapid growth."

According to Young and Evans (1981), even under optimum conditions germination of cliffrose rarely exceeds 60%. They credit the lack of success to the amount and type of dormancy found in the seeds and suggest that an ideal field stratification environment for cliffrose seeds is one with constant moisture near field capacity and a temperature of 0 to 5 C. Therefore, the environmental requirements for success in cliffrose germination and the potential response of cheatgrass when these conditions are obtained may well explain the apparent negative relationship of cliffrose with average annual rainfall. Competition between cliffrose seedlings and cheatgrass may become highly intense during years of increased average annual precipitation and therefore help explain the lack of cliffrose establishment on our sites in recent years.

Other introduced annuals of prevalence were madwort (averaging 3.5% cover) and Japanese chess (*Bromus japonicus*) (averaging only 1%, but found well established on some sites). Original data (collected in the fall) showed storksbill (*Erodium cicutarium*) to play a minor role in the cover composition (Table 4). However, when sites were reexamined in the spring, some communities had significant quantities of storksbill and jagged chickweed in their understory.

Disturbance: Practically all 10 study sites have a history of extensive grazing pressure by sheep, cattle, and wildlife. Because they furnish food and shelter, cliffrose stands would tend to concentrate livestock and wildlife. Such disturbance would open the sites to cheatgrass invasion and establishment.

Studies conducted by Cook and Harris (1952) showed that when cheatgrass was in the dough stage (usually around May) and turning purple, sheep ate the entire plant down to one-half inch above the ground. Hull and Pechanec (1947) observed that cattle and horses ate dry cheatgrass readily if ample water were available, and both cattle and sheep ate dry cheatgrass in the winter. Stewart and Hull (1949) estimated that cheatgrass utilization as low as 35 to 40% would allow reestablishment of perennial cover. Increased utilization and disturbance of cheatgrass, due to the higher concentration of grazing animals, would most likely aid in the establishment of cliffrose by trampling its seed into the ground and reducing the competition for moisture between cliffrose seedlings and cheatgrass. However, since livestock grazing permits on most of the study sites were revoked in 1957, cliffrose establishment by increasing utilization of cheatgrass is not a good choice to explain the success or failure of seedling success. In fact, 1957 is the same year the histogram in Figure 6 shows the success of cliffrose seedlings beginning to decline.

Fire: Many of the exotic annuals grow in dense stands where they generally complete their life cycle early in the growing season and then become dry and susceptible to summer wildfires. Young et al. (1972) say, "The fuel provided by early maturing, highly flammable alien annuals contributes to the incidence and spread of these species." McCulloch's (1969) study showed cliffrose stands to be drastically reduced by fire. Fire carried by a dense stand of dried exotic annuals was responsible for destroying over half the cliffrose community on the study plot in Springville. Where the fire had swept, no cliffrose plants survived.

CLIFFROSE MANAGEMENT.—Cliffrose seedlings, when allowed relative freedom from annual competition throughout the first growing season, have highly increased establishment success. It is believed decadent cliffrose communities could be rejuvenated by reducing competition as seldom as once every 10 to 15 years.

Areas that might be considered for effective competition reduction are biological, mechanical, and chemical. Concentrated grazing to increase soil disturbance and cheatgrass utilization may in some areas have practical application. Increasing seedling success by mechanically placing scattered soil scalps within cliffrose communities could also prove to be an effective managment practice.

In the past, few methods have been successful in controlling cheatgrass and other exotic annuals (Young et al. 1972). In recent years cheatgrass control with chemicals has received attention. Though not feasible for extensive rangeland control, chemicals have real promise in enhancement of perennial grasses and browse species (Klemmedson and Smith 1964).

SUMMARY AND CONCLUSIONS

Data indicate cliffrose site preference in central Utah is highly consistent. Cliffrose communities are generally located on steeper slopes which are exposed to environmental extremes. Soils associated with cliffrose are relatively low in most macronutrients and some micronutrients. Vegetative composition is dominated by exotic annuals (predominantly cheatgrass) with shrubs (predominantly cliffrose) being the next important life form. From the data it appears that competition for resources is less severe between mature cliffrose plants and annuals than between cliffrose and perennials. The nutrient concentrations in cliffrose tissue, relative to soil concentrations, indicate nutrient pumping has been implemented for adaptation to nutrient-poor sites. Age distribution of cliffrose shows a decline in successful seedling establishment over the last 25 years. Data from this study and others indicate that the major contributing factor responsible for the decline is competitive exclusion by exotic annuals (mainly cheatgrass). Destruction of cliffrose by fire due to dense stands of exotic annuals may also explain how exotic annuals eliminate plants competing with them for environmental resources. The negative factors influencing deterioration of cliffrose populations are most likely amplified in central Utah when cliffrose is at the northern edge of its natural range. Since habitat for cliffrose in central Utah is less than optimal, if cliffrose communities are to be maintained or enhanced, special attention to their management must be considered and implemented.

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ALPINE VASCULAR FLORA OF THE RUBY RANGE, WEST ELK MOUNTAINS, COLORADO

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ABSTRACT.—The Ruby Range is a northern extension of the West Elk Mountains of west central Colorado. Composed primarily of sedimentary rocks, the range is heavily faulted and intruded by many dikes and sills. Eight study areas, selected as representative of the major topographic features of the range, were analyzed floristically. A vascular flora of 220 species in 111 genera and 35 families is reported. The phytogeographic distribution of the flora is primarily alpine and western North American. The flora of the Ruby Range shows a 74% similarity to the flora of the San Juan Mountains to the southwest.

The Ruby Range, a northern extension of the West Elk Mountains (Prather 1982) of west central Colorado, is west of the Continental Divide between 107 degrees 05 minutes and 107 degrees 07 minutes West longitude and 38 degrees 52 minutes and 39 degrees North latitude. This discrete range extends 15.2 km northward from its southern boundary, 18.5 km northwest of Crested Butte, Gunnison County. In outline the range resembles the letter *h* with the vertical line being formed on the west by a series of 11 mountain peaks ranging in elevation from 3,573 to 3,982 m. The curved part of the letter represents an escarpment and its southeastern terminus ranges from 3,664 to 3,780 m. Glacial effects are evident in the present alpine landscape as cirques, tarns, hanging valleys, basins, rock steps, and broad U-shaped valleys in the lower elevations.

The Ruby Range is composed primarily of sedimentary rocks intruded by many dikes and sills. The sedimentary formations include: Mancos Shale, a silty marine shale interbedded with silty sandstone, sandy limestone, and carbonaceous shale of Upper Cretaceous age in the north; Mesa Verde, interbedded sandstone, shale, coal, and carbonaceous shale of Upper Cretaceous age in the central part; and Wasatch, evenly bedded sandstone, siltstone, and conglomerate of Eocene age in the south. The Mancos Shale is locally metamorphosed to hornfels, whereas the Wasatch is generally metamorphosed to quartzite, argillite, and silty and argillaceous hornfels. A large number of dikes and sills composed of either quartz monzonite porphyry, granodiorite porphyry, or dacite porphyry are intruded into the sedimentary formations. Stocks of quartz monzonite porphyry form the summits of four of the mountains in the range (Gaskill et al. 1967). There are numerous fault zones and talus deposits in the range. A floristic study of the subalpine and alpine zones in Robinson Basin was made by Bathke (1968).

Collections were made in the Ruby Range during the summers 1980–1985. Nomenclature in the checklist follows Kartesz and Kartesz (1980). Voucher specimens are deposited in CU-Denver. Phytogeographic abbreviations used in the annotated checklist of vascular species are identified in the discussion section.

STUDY AREAS

Eight study areas representative of the major topographic features and distributed throughout the length of the Ruby Range were selected. Northeast-facing cirque basins of Mount Owen, Purple Peak, and Augusta Mountain are the highest in elevation, ranging from 3,660 to 3,843 m. Baxter, Robinson, and Redwell basins are drainage basins of the Slate River, a tributary of the Gunnison River. The elevational range of the upper parts of these basins is 3,556 to 3,599 m. Scarp Ridge, a northwest-southeast–trending escarpment ranges in elevation from 3,664 to 3,725 m. The south- and southwest-facing convex slopes of Mount Emmons, which forms the southeast terminus of Scarp Ridge, range in elevation from 3,698 to 3,780 m.

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Climatic data are lacking from the study area. The nearest U.S. Weather Bureau station is Crested Butte at 2,701 m elevation to the east. Only generalized climatic information for the Ruby Range can be extrapolated from this station. Two precipitation maxima occur: July to September, and January (Langenheim 1962). Heavy snowfall in the winter renders the area inaccessible from November through June. Permanent snowbanks are common on northeast-facing exposures in the higher elevations. The prevailing winds are from the west and southwest. Wind velocities approaching 92 kph are not uncommon in the alpine throughout the summer (Bathke 1968).

PLANT COMMUNITIES

Meadow Communities

The moist meadow community type is most representative of the tundra in the Ruby Range. This contrasts with the predominant dry meadows of the Front Range and correlates with the San Juan Mountains which, like the Ruby Range, experience a higher moisture regime (Hartman and Rottman 1985). In many places the uniformity of the turf meadow is interrupted by talus deposits and tailings associated with old mining activity. Moist meadow communities on slopes are dominated by *Deschampsia caespitosa* and *Geum rossii* var. *turbinatum*; whereas *Carex nigricans* and *Juncus drummondii* dominate the community type in flat areas.

Dry meadow communities occur on steep, rocky, convex slopes which experience early snowmelt or adjacent to bedrock outcrops. The most frequent dominants include *Agropyron trachycaulum* var. *latiglume*, *Danthonia intermedia*, *Geum rossii* var. *turbinatum*, and *Ivesia gordonii*. *Kobresia myosuroides*, the overwhelming dominant of dry meadows and climatic climax species of the Front Range (Marr 1961, Eddleman and Ward 1984), is highly restricted in occurrence in the Ruby Range. Langenheim (1962) found the same to be true in the adjacent Elk Mountains near Crested Butte. *Carex elynoides*, a dry meadow dominant and substitute for *Kobresia* in the San Juan Mountains (Hartman and Rottman 1985), is restricted in occurrence to fellfields in the Ruby Range.

The dominants found in wet meadows adjacent to ponds are *Caltha leptosepala*, *Carex illota*, and *Carex praeceptorum*. On slopes and in association with rivulets the wet meadow dominants are *Caltha leptosepala* and *Corydalis caseana* ssp. *brandegii*.

Fellfield Community

Fellfields are restricted to ridgetops and the top surface of bedrock outcrops. This community type may show a lack of dominants or may have *Ivesia gordonii* as the dominant species. The typical fellfield cushion plant community, dominated by *Paronychia pulvinata* and *Phlox caespitosa* ssp. *condensata*, on windswept sites of the Front Range (Cox 1933, Eddleman and Ward 1984) and Sangre de Cristo Range (Soil Conservation Service 1979) is absent in the Ruby Range.

Talus Community

Talus communities in the Ruby Range, like those of the Mosquito Range (Hartman and Rottman 1985), are characterized by a lack of dominants and a high diversity of total species present, reflecting the opportunistic nature of many tundra species (Schaack 1983). Any number of 83 species may be found in various talus communities.

Krummholz Community

Timberline, in the form of krummholz, is variable ranging from 3,538 to 3,729 m with the lower elevations found on easterly exposures and the higher on southerly exposures. This ecotonal community has representative species from both the alpine and subalpine zones. Krummholz conifers, *Abies lasiocarpa* and *Picea engelmannii*, are equally co-dominant.

Shrub Tundra Community

The shrub tundra community is very patchy and restricted to moist depressions and drainage areas. This community is dominated by thickets of *Salix brachycarpa* and *Salix glauca* var. *villosa* which exert a primary influence on the surrounding environment and associated species.

DISCUSSION

The alpine flora of the Ruby Range consists of 220 vascular plants: 213 species representing 104 genera of angiosperms, 3 genera and 3 species of gymnosperms, and 4 genera and 4 species of pteridophytes. The family with the greatest number of species is Asteraceae with 34 species. Other families with a large representation are Cyperaceae, Poaceae, Brassicaceae, Caryophyllaceae, Saxifragaceae, and Rosaceae with 23, 19, 17, 15, 12, and 11 taxa, respectively.

In comparing the seven leading families found in the Ruby Range to those found in the San Juan Mountains, southwestern Colorado (Hartman and Rottman 1985); Mosquito Range, north central Colorado (Hartman and Rottman 1985); and Indian Peaks area of the Front Range, northern Colorado (Komarkova 1976), only the exclusion of the Scrophulariaceae and inclusion of the Rosaceae are noted; however, the rank order varies somewhat with each range. Although there is a tendency to emphasize differences in community structure and dominants in this study and other studies in Colorado, much similarity is seen in the floristic inventories from the various areas. The greatest similarity, 74%, occurs between the Ruby Range and the San Juan Mountains and a slightly lower 70% with the Indian Peaks area of the Front Range. The lowest similarity in vascular plant inventories, 66%, occurs between this study and the Mosquito Range.

Phytogeography

Table 1 shows the phytogeographic distribution of the flora. Four elements are recognized, each of which may be combined with more specific geographic subelements (Komarkova 1976). Several of these subelements should be defined. The Rocky Mountains subelement includes the Northern Rocky Mountain province south to the Laramie Basin in Wyoming. The Southern Rocky Mountains subelement includes southern Wyoming, Colorado, New Mexico, and Arizona. The Colorado subelement represents species which are endemic to Colorado. Phytogeographic determinations for taxa are taken from Porsild (1957), Weber (1965), Munz and Keck (1970), Komarkova (1976), Cronquist et al. (1977), Porsild and Cody (1980), and Moss (1983).

Table 1. Affinities of the flora elements in the Ruby Range, Colorado. Abbreviations following each unit are cited in the annotated checklist.

Element	Abbreviation	Percent of taxa
ELEMENT		
Boreal montane	BM	24.1
Montane	M	16.8
Arctic alpine	AA	23.6
Alpine	A	35.5
GEOGRAPHIC SUBELEMENT		
Circumpolar	C	17.7
North American	NA	12.3
Western North American	WNA	32.3
Rocky Mountains	RM	14.5
Southern Rocky Mountains	SRM	11.8
Colorado	CO	1.4
North American–Asiatic	NAA	8.6
North American–European	NAE	1.4

As may be seen from the percentages given, the largest part of the vascular flora is made up of alpine species (35.5%) and western North American species (32.3%). The circumpolar subelement (17.7%), which is closely identified with the arctic-alpine element, is a second important component of the flora. With the exception of seven species, the North American–Asiatic subelement is linked also with the arctic-alpine element. In the montane element the Rocky Mountain species are nearly double the Southern Rocky Mountain species, whereas the latter two are nearly equal in the alpine element. A stronger affinity between the Ruby Range alpine flora and the Asiatic alpine flora than to the European alpine flora is indicated by the higher percentage of North American–Asiatic species (8.6%) in relation to North American–European species (1.4%). This appears to be the case in all ranges of Colorado studied floristically.

A comparison of phytogeographic analyses of the Ruby Range shows a higher boreal-montane and montane representation and a concomitantly lower arctic-alpine representation in this study than in the San Juan Mountains (Hartman and Rottman 1985). This same trend is seen in the Mosquito Range comparison (Hartman and Rottman 1985). The western North American subelement is higher, however, in the Ruby Range than in either the San Juan Mountains or Mosquito Range. There is less than 0.2% difference in the Southern Rocky Mountain species between all three mountain ranges.

A comparison of the phytogeographic analyses of this study with the Indian Peaks area of the Front Range, northern Colorado

(Komarkova 1976), indicates a decrease in the number of arctic-alpine (5.4%) and alpine (5.0%) species. Among the subelements there is a decrease in circumpolar (8.1%) and North American–Asiatic (2.1%) species and a small increase (3.7%) in western North American species.

Colorado Endemics

There are only three endemic species, Colorado subelement, found in the Ruby Range: *Draba spectabilis* var. *oxyloba*, *Potentilla subjuga* var. *subjuga*, and *Senecio soldanella*. This number is lower than in the more northerly Mosquito Range and Indian Peaks area of the Front Range and fails to support the statement of Major and Bamberg (1967) that endemism increases in a southerly direction.

ANNOTATED CHECKLIST OF VASCULAR PLANT SPECIES

PTEROPHYTA

Selaginellaceae

***Selaginella densa* Rydb.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, talus, and patterned ground. A/WNA.

Adiantaceae

***Cryptogramma crispa* (L.) Br. ex Hook. ssp. *acrostichoides* (R. Br.) Hulten.** Infrequent; dry and moist meadows, dry ledge, and talus. BM/NAA.

Aspleniaceae

***Athyrium destentifolium* Tausch ex Opiz var. *americanum* (Butters) Boivin.** Rare; talus and disturbed area. BM/NAA.

***Cystopteris fragilis* (L.) Bernh.** Infrequent; moist and wet meadows, and moist ledges. AA/C.

CONIFEROPHYTA

Pinaceae

***Abies lasiocarpa* (Hook.) Nutt.** Rare; krummholz. BM/WNA.

***Juniperus communis* L.** Rare; krummholz. BM/C.

***Picea engelmannii* Parry ex Engelm.** Rare; krummholz. BM/WNA.

ANTHOPHYTA - DICOTYLEDONEAE

Apiaceae

***Angelica grayi* Coult. & Rose.** Infrequent; moist and wet meadows, shrub tundra, talus, and disturbed area. A/SRM.

***Ligusticum porteri* Coult. & Rose.** Rare; moist meadow and talus. M/RM.

***Oreoxis alpina* (Gray) Coult. & Rose.** Rare; dry meadow. A/SRM.

***Oreoxis bakeri* Coult. & Rose.** Infrequent; dry and moist meadows, dry and moist ledges, and rivulet. A/SRM.

***Oxypolis fendleri* (Gray) Heller.** Rare; moist ledge and rivulet. M/SRM.

***Pseudocymopterus montanus* (Gray) Coult. & Rose.** Infrequent; dry and moist meadows, fellfield, shrub tundra, krummholz, and disturbed area. M/SRM.

Asteraceae

***Achillea millefolium* L. var. *lanulosa* (Nutt.) Piper.** Infrequent; dry and moist meadows, shrub tundra, krummholz, and talus. A/WNA.

***Agoseris aurantiaca* (Hook.) Greene.** Infrequent; moist meadow, fellfield, and krummholz. BM/WNA.

***Agoseris glauca* (Pursh) Raf.** Infrequent; dry and moist meadows, dry ledge, shrub tundra, talus, and disturbed area. BM/NA.

***Antennaria alpina* (L.) Gaertn.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, and talus. AA/NAE.

***Antennaria microphylla* Rydb.** Rare; talus and disturbed area. BM/NA.

***Arnica mollis* Hook.** Common; dry, moist and wet meadows, dry and moist ledges, shrub tundra, krummholz, and disturbed area. BM/NA.

***Arnica rydbergii* Greene.** Very rare; dry meadow. BM/WNA

***Artemisia ludoviciana* Nutt. ssp. *incompta* (Nutt.) Keck.** Very rare; dry meadow. M/WNA.

***Artemisia scopulorum* Gray.** Ubiquitous; dry and moist meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, rivulet, and disturbed area. A/RM.

***Aster foliaceus* Lindl. var. *apricus* Gray.** Infrequent; moist and wet meadows, fellfield, moist ledge, shrub tundra, and disturbed area. A/WNA.

***Chaenactis alpina* (Gray) H. E. Jones.** Infrequent; dry meadow, fellfield, and talus. M/WNA.

***Erigeron coulteri* Porter.** Rare; moist meadow and shrub tundra. BM/WNA.

***Erigeron elatior* (Gray) Gray.** Rare; dry meadow and talus. M/SRM.

***Erigeron melanocephalus* A. Nels.** Infrequent; moist and wet meadows, fellfield, moist ledge, and talus. A/SRM.

***Erigeron pinnatisectus* (Gray) A. Nels.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, and talus. A/SRM.

***Erigeron peregrinus* (Pursh) Greene.** Common; dry, moist and wet meadows, dry ledge, shrub tundra, krummholz, and rivulet. BM/WNA.

***Erigeron simplex* Greene.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, and talus. A/WNA.

***Haplopappus parryi* Gray.** Very rare; shrub tundra. M/SRM.

***Haplopappus pygmaeus* (Torr. & Gray) Gray.** Very rare; fellfield. A/RM.

***Heterotheca fulcrata* (Greene) Shinners.** Infrequent; dry meadow, dry ledge, and talus. M/RM.

***Hieracium gracile* Hook.** Infrequent; dry and moist meadows, fellfield, dry and moist ledges, and krummholz. A/WNA.

Hymenoxys grandiflora **(Torr. & Gray ex Gray) Parker.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz and disturbed area. A/RM.

Senecio amplectens **Gray var. *amplectens*.** Infrequent; wet meadow, moist ledge, talus, rock debris habitats, snowbank, and disturbed area. M/RM.

Senecio amplectens **Gray var. *holmii*** **(Greene) Harrington.** Infrequent; dry meadow, fellfield, dry ledge, talus, and disturbed area. M/RM.

Senecio atratus **Greene.** Infrequent; dry and wet meadows and krummholz. A/SRM.

Senecio crassulus **Gray.** Ubiquitous; dry, moist and wet meadows, moist ledge, shrub tundra, krummholz, talus, rivulet, snowbank, and disturbed area. BM/WNA.

Senecio dimorphophyllus **Greene.** Infrequent; moist and wet meadows, dry and moist ledges, and shrub tundra. M/RM.

Senecio soldanella **Gray.** Rare; fellfield. A/CO.

Senecio taraxacoides **(Gray) Greene.** Very rare; talus. A/SRM.

Senecio triangularis **Hook.** Rare; moist meadow and moist ledge. BM/WNA.

Senecio werneriifolius **(Gray) Gray.** Common; dry and moist meadows, fellfield, dry ledge, talus, rivulet, and disturbed area. M/RM.

Solidago spathulata **DC. var. *nana*** **(Gray) Cronq.** Common; dry and moist meadows, fellfield, dry ledge, shrub tundra, krummholz, and talus. A/WNA.

Taraxacum ceratophorum **(Ledeb.) DC.** Infrequent; dry meadow, talus, and disturbed area. AA/C.

Taraxacum lyratum **(Ledeb.) DC.** Very rare; dry ledge. AA/NAA.

Boraginaceae

Mertensia bakeri **Greene.** Infrequent; dry meadow, fellfield, dry ledge, and disturbed area. A/SRM.

Mertensia ciliata **(James ex Torr.) G. Don.** Infrequent; moist and wet meadows, shrub tundra, krummholz, and rock debris habitats. BM/WNA.

Brassicaceae

Arabis drummondii **Gray.** Common; dry and moist meadows, fellfield, dry ledge, krummholz, talus, and disturbed area. BM/NA.

Arabis lemmonii **S. Wats.** Very rare; talus. A/WNA.

Cardamine cordifolia **Gray.** Infrequent; wet meadow, shrub tundra, and rivulet. BM/WNA.

Draba aurea **Vahl.** Infrequent; fellfield, talus, and disturbed area. AA/C.

Draba crassa **Rydb.** Rare; dry ledge. A/RM.

Draba crassifolia **Graham.** Infrequent; moist meadow, fellfield, moist ledge, talus, and disturbed area. AA/NAE.

Draba fladnizensis **Wulfen.** Rare; fellfield and talus. AA/C.

Draba incerta **Payson.** Rare; patterned ground and disturbed area. AA/WNA.

Draba nivalis **Lilj.** Very rare; dry ledge. AA/C.

Draba oligosperma **Hook.** Very rare; fellfield. AA/WNA.

Draba spectabilis **Greene var. *oxyloba*** **(Greene) Gilg. ex O. E. Schulz.** Infrequent; dry and moist meadows and fellfield. A/CO.

Draba spectabilis **Greene var. *spectabilis*.** Rare; moist meadow and talus. M/RM.

Draba streptocarpa **Gray var. *streptocarpa*.** Rare; dry ledge. A/SRM.

Erysimum nivale **(Greene) Rydb.** Infrequent; dry meadow, fellfield, dry ledge, and disturbed area. A/SRM.

Rorippa curvipes **Greene.** Infrequent; moist and wet meadows and disturbed area. A/RM.

Smelowskia calycina **(Steph.) C. A. Mey. ex Ledeb.** Infrequent; dry and moist meadows, fellfield, dry ledge, krummholz, and patterned ground. AA/NAA.

Thlaspi montanum **L.** Ubiquitous; dry, moist and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, snowbank, and disturbed area. A/C.

Campanulaceae

Campanula rotundifolia **L.** Infrequent; dry and moist meadows, fellfield, dry ledge, and krummholz. BM/C.

Campanula uniflora **L.** Rare; dry meadow and dry ledge. AA/C.

Caryophyllaceae

Arenaria congesta **Nutt. ex Torr. & Gray.** Infrequent; dry and moist meadows, fellfield, dry ledge, and krummholz. M/WNA.

Cerastium earlei **Rydb.** Common; dry and moist meadows, fellfield, dry ledge, shrub tundra, talus, patterned ground, and disturbed area. A/RM.

Minuartia biflora **(L.) Schinz & Thellung.** Rare; fellfield and dry ledge. AA/C.

Minuartia obtusiloba **(Rydb.) House.** Infrequent; dry and moist meadows, fellfield, and dry and moist ledges. AA/NAA.

Minuartia rubella **(Wallenb.) Hiern.** Infrequent; dry and moist meadows, fellfield, dry ledge, krummholz, and patterned ground. AA/C.

Minuartia stricta **(Sw.) Hiern.** Very rare; moist ledge. AA/C.

Moehringia lateriflora **(L.) Fenzl.** Rare; shrub tundra and krummholz. AA/C.

Moehringia macrophylla **(Hook.) Fenzl.** Very rare; shrub tundra. BM/NA.

Sagina saginoides **(L.) Karst.** Infrequent; moist meadow, fellfield, moist ledge, and disturbed area. AA/C.

Silene acaulis **(L.) Jacq. var. *subacaulis*** **(F. N. Williams) C. L. Hitchc. & Maguire.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, talus, patterned ground, and disturbed area. AA/NAA.

Silene drummondii **Hook.** Rare; dry meadow and krummholz. BM/NA.

Silene kingii **(S. Wats.) Bocquet.** Rare; moist meadow and fellfield. A/SRM.

Silene uralensis **(Rupr.) Bocquet.** Very rare; fellfield. AA/C.

Stellaria longipes **Goldie.** Rare; krummholz and talus. BM/NA.

Stellaria umbellata **Turcz. ex Kar. & Kir.** Infrequent; moist and wet meadows, shrub tundra, talus, and disturbed area. A/NAA.

Celastraceae

Pachistima myrsinites **(Pursh) Raf.** Very rare; talus. M/WNA.

Crassulaceae

Sedum integrifolium **(Raf.) A. Nels. ex Coult. & A. Nels.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, rock debris habitats, rivulet, and disturbed area. AA/NAA.

Sedum lanceolatum **Torr.** Common; dry and moist meadows, fellfield, dry ledge, krummholz, talus, and patterned ground. A/WNA.

Sedum rhodanthum **Gray.** Infrequent; moist and wet meadows, moist ledge, and shrub tundra. A/RM.

Ericaceae

Arctostaphylos uva-ursi **(L.) Spreng.** Very rare; moist ledge. BM/NA.

Gaultheria humifusa **(Graham) Rydb.** Very rare; moist ledge. BM/WNA.

Vaccinium caespitosum **Michx.** Common; dry and moist meadows, fellfield, dry and moist ledges, shrub tundra, and krummholz. BM/NA.

Vaccinium myrtillus **L. ssp.** ***oreophilum*** **(Rydb.) Love, Love & Kapoor.** Very rare; shrub tundra. BM/C.

Fabaceae

Lupinus argenteus **Pursh.** Infrequent; dry meadow, dry ledge, shrub tundra, and talus. M/WNA.

Trifolium dasyphyllum **Torr. & Gray.** Infrequent; dry meadow, fellfield, dry ledge, krummholz, and talus. A/RM.

Trifolium nanum **Torr.** Infrequent; dry meadow, fellfield, dry ledge, and patterned ground. A/RM.

Trifolium parryi **Gray.** Ubiquitous; dry, moist, and wet meadows, dry and moist ledges, shrub tundra, krummholz, talus, snowbank, and disturbed area. A/RM.

Gentianaceae

Gentiana algida **Pallas.** Infrequent; dry and moist meadows, fellfield, and shrub tundra. AA/NAA.

Gentiana calycosa **Griseb.** Rare; moist meadow and krummholz. A/WNA.

Gentiana prostrata **Haenke ex Jacq.** Very rare; moist ledge. AA/NAA.

Gentianella amarella **(L.) Borner.** Infrequent; dry and moist meadows, fellfield, dry ledge, and shrub tundra. BM/C.

Gentianella tenella **(Rottb.) Borner.** Infrequent; dry and moist meadows, and moist ledge. AA/C.

Gentianopsis barbellata **(Engelm.) Iltis.** Very rare; krummholz. A/SRM.

Gentianopsis thermalis **(Kuntze) Iltis.** Infrequent; dry, moist, and wet meadows, and moist ledge. A/RM.

Swertia perennis **L.** Rare; moist meadow and shrub tundra. A/C.

Geraniaceae

Geranium richardsonii **Fisch. & Trautv.** Rare; dry ledge and krummholz. M/WNA.

Hydrophyllaceae

Phacelia heterophylla **Pursh.** Rare; fellfield and talus. M/WNA.

Phacelia sericea **(Graham) Gray.** Infrequent; dry meadow, krummholz, talus, and disturbed area. A/WNA.

Onagraceae

Epilobium anagallidifolium **Lam.** Infrequent; moist and wet meadows, talus, rivulet, and disturbed area. AA/C.

Orobanchaceae

Orobanche uniflora **L.** Very rare; moist meadow. BM/NA.

Papaveraceae

Corydalis caseana **Gray ssp.** ***brandegii*** **(S. Wats.) G. B. Ownbey.** Common; moist and wet meadows, moist ledge, shrub tundra, krummholz, talus, rivulet, snowbank, and disturbed area. M/SRM.

Polemoniaceae

Polemonium delicatum **Rydb.** Very rare; krummholz. M/SRM.

Polemonium viscosum **Nutt.** Infrequent; dry and moist meadows, talus, and disturbed area. A/WNA.

Polygonaceae

Eriogonum jamesii **Benth. var.** ***xanthum*** **(Small) Reveal.** Very rare; talus. A/WNA.

Eriogonum umbellatum **Torr.** Infrequent; dry meadow, fellfield, dry ledge, and talus. M/WNA.

Oxyria digyna **Hill.** Common; moist meadow, fellfield, dry ledge, talus, rock debris habitats,rivulet, and disturbed area. AA/C.

Polygonum bistortoides **Pursh.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, patterned ground, rivulet, and disturbed area. A/WNA.

Polygonum douglasii **Greene.** Very rare; dry meadow. BM/NA.

Polygonum viviparum **L.** Infrequent; dry and moist meadows, dry and moist ledges, shrub tundra, and rock crevice. AA/C.

Portulacaceae

Claytonia lanceolata **Pursh.** Very rare; talus. M/WNA.

Claytonia megarhiza **(Gray) Parry ex S. Wats.** Infrequent; fellfield, dry ledge, talus, patterned ground, and rock debris habitats. A/RM.

Lewisia pygmaea **(Gray) B. L. Robins.** Common; dry, moist, and wet meadows, fellfield, moist ledge, shrub tundra, talus, and rivulet. A/WNA.

Primulaceae

Androsace septentrionalis **L.** Infrequent; dry and moist meadows, fellfield, talus, and patterned ground. AA/C.

Primula parryi **Gray.** Infrequent; moist and wet meadows, moist ledge, talus, and rivulet. A/RM.

Ranunculaceae

Anemone narcissiflora **L. ssp.** ***zephyra*** **(A. Nels.) Love, Love & Kapoor.** Common; dry, moist, and wet meadows, fellfield, moist ledge, krummholz, and shrub tundra. A/SRM.

Aquilegia coerulea **James.** Infrequent; dry meadow, fellfield, dry ledge, shrub tundra, krummholz, and talus. M/RM.

***Caltha leptosepala* DC.** Infrequent; moist and wet meadows, moist ledge, shrub tundra, and rivulet. A/WNA.

***Delphinium barbeyi* (Huth) Huth.** Very rare; talus. M/SRM.

***Ranunculus alisamifolius* Geyer ex Benth. var. *montanus* S. Wats.** Infrequent; moist and wet meadows, moist ledge, shrub tundra, and rivulet. BM/WNA.

***Ranunculus eschscholtzii* Schlect.** Infrequent; moist and wet meadows and moist ledge. AA/NAA.

***Ranunculus macauleyi* Gray.** Common; moist and wet meadows, moist ledge, talus, rivulet, snowbank, and disturbed area. A/SRM.

***Trollius laxus* Salisb. ssp. *albiflorus* (Gray) Love, Love & Kapoor.** Infrequent; moist and wet meadows, and shrub tundra. BM/WNA.

Rosaceae

***Fragaria vesca* L. ssp. *americana* (Porter) Staudt.** Rare; moist meadow and krummholz. BM/NA.

***Geum rossii* (R. Br.) Ser. var. *turbinatum* (Rydb.) C. L. Hitchc.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, patterned ground, rivulet, snowbank, and disturbed area. AA/NAA.

***Ivesia gordonii* (Hook.) Torr. & Gray.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, talus, and disturbed area. M/WNA.

***Potentilla diversifolia* Lehm.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, patterned ground, rivulet, snowbank, and disturbed area. A/WNA.

***Potentilla fruticosa* L. ssp. *floribunda* (Pursh) Elkington.** Infrequent; dry and moist meadows, fellfield, dry ledge, and talus. BM/C.

***Potentilla nivea* L.** Infrequent; dry meadow, fellfield, dry ledge, and patterned ground. AA/C.

***Potentilla ovina* Macoun.** Infrequent; fellfield, dry and moist ledges. M/WNA.

***Potentilla rubricaulis* Lehm.** Rare; dry meadow and fellfield. AA/NA.

***Potentilla subjuga* Rydb. var. *subjuga*.** Rare; dry meadow and dry ledge. A/CO.

***Rubus idaeus* L. ssp. *sachalinensis* (Levi.) Focke.** Very rare; talus. BM/NAA.

***Sibbaldia procumbens* L.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, rivulet, and disturbed area. AA/C.

Salicaceae

***Salix arctica* Pallas.** Infrequent; dry and moist meadows and patterned ground. A/WNA.

***Salix brachycarpa* Nutt.** Infrequent; moist ledge, shrub tundra, and krummholz. BM/NA.

***Salix glauca* L. var. *villosa* (Hook.) Anderss.** Rare; shrub tundra and krummholz. BM/WNA.

***Salix planifolia* Pursh.** Rare; moist ledge and shrub tundra. BM/NA.

***Salix reticulata* L. ssp. *nivalis* (Hook.) Love, Love & Kapoor.** Infrequent; dry and moist meadows, fellfield, dry ledge, and shrub tundra. A/WNA.

Saxifragaceae

***Heuchera parvifolia* Nutt. ex Torr. & Gray.** Rare; moist meadow and dry ledge. M/RM.

***Ribes coloradense* Coville.** Very rare; dry ledge. M/SRM.

***Ribes montigenum* McClatchie.** Very rare; krummholz. BM/WNA.

***Saxifraga adscendens* L. ssp. *oregonensis* (Raf.) Bacig.** Very rare; moist meadow. AA/NAE.

***Saxifraga bronchialis* L. ssp. *austromontana* (Wieg.) Piper.** Infrequent; fellfield, dry ledge, krummholz, talus, and patterned ground. A/WNA.

***Saxifraga caespitosa* L. ssp. *delicatula* (Small) Porsild.** Very rare; patterned ground. AA/C.

***Saxifraga chrysantha* Gray.** Very rare; patterned ground. AA/NAA.

***Saxifraga debilis* Engelm. ex Gray.** Infrequent; moist meadow, fellfield, dry and moist ledges, and talus. A/RM.

***Saxifraga flagellaris* Sternb. & Willd. ssp. *platysepala* (Trautv.) Porsild.** Rare; fellfield and patterned ground. A/SRM.

***Saxifraga odontoloma* Piper.** Rare; wet meadow and moist ledge. BM/WNA.

***Saxifraga oregana* T. J. Howell ssp. *montanensis* (Small) C. L. Hitchc.** Infrequent; moist and wet meadows and shrub tundra. M/WNA.

***Saxifraga rhomboidea* Greene.** Common; dry and moist meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, and rivulet. A/WNA.

Scrophulariaceae

***Besseya alpina* (Gray) Rydb.** Infrequent; dry and moist meadows, fellfield, dry ledge, talus, and patterned ground. A/SRM.

***Castilleja occidentalis* Torr.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, and disturbed area. A/RM.

***Castilleja rhexifolia* Rydb.** Infrequent; moist meadow, shrub tundra, and rivulet. BM/WNA.

***Mimulus guttatus* DC.** Rare; moist ledge and disturbed area. BM/NA.

***Pedicularis bracteosa* Benth. var. *paysoniana* (Pennell) Cronq.** Rare; moist meadow and shrub tundra. M/RM.

***Pedicularis groenlandica* Retz.** Infrequent; moist and wet meadows, moist ledge, shrub tundra, and rivulet. AA/NA.

***Pedicularis parryi* Gray.** Infrequent; dry and moist meadows, fellfield, dry and moist ledges, and shrub tundra. A/RM.

***Penstemon whippleanus* Gray.** Common; dry and moist meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, and talus. M/RM.

***Veronica wormskjoldii* Roemer & Shultes.** Common; dry, moist, and wet meadows, dry and moist ledges, shrub tundra, krummholz, rivulet, and disturbed area. AA/NA.

Valerianaceae

***Valeriana capitata* Pallas ex Link.** Very rare; fellfield. AA/NAA.

***Valeriana edulis* Nutt. ex Torr. & Gray.** Rare; moist meadow and dry ledge. BM/WNA.

Violaceae

***Viola adunca* Sm. ssp. *bellidifolia* (Greene) Harrington.** Infrequent; moist meadow, fellfield, and moist ledge. BM/NA.

Viola nuttallii **Pursh.** Rare; dry meadow and dry ledge. M/WNA.

ANTHOPHYTA - MONOCOTYLEDONEAE

Cyperaceae

Carex albonigra **Mackenzie.** Infrequent; moist meadow, moist ledge, shrub tundra, and talus. AA/WNA.

Carex aquatilis **Wahlenb.** Rare; wet meadow. AA/C.

Carex arapahoensis **Clokey.** Rare; dry meadow and rock debris habitats. A/SRM.

Carex brevipes **W. Boott.** Very rare; moist meadow. BM/NA.

Carex brunnescens **(Pers.) Poir.** Very rare; wet meadow. BM/C.

Carex ebenea **Rydb.** Common; dry, moist, and wet meadows, fellfield, moist ledge, shrub tundra, talus, and disturbed area. A/RM.

Carex elynoides **Holm.** Rare; fellfield. A/WNA.

Carex foenea **Willd.** Infrequent; dry ledge, krummholz, and talus. BM/NA.

Carex geyeri **Boott.** Very rare; krummholz. M/WNA.

Carex haydeniana **Olney.** Infrequent; dry and moist meadows, dry ledge, talus, and disturbed area. A/WNA.

Carex heteroneura **W. Boott var. *chalciolepis* (Holm) F. J. Herm.** Common; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, talus, and disturbed area. A/WNA.

Carex heteroneura **W. Boott var. *epapillosa* (Mackenzie) F. J. Herm.** Very rare; dry meadow. M/WNA.

Carex illota **Bailey.** Rare; moist and wet meadows. A/WNA.

Carex nelsonii **Mackenzie.** Rare; fellfield and dry ledge. A/SRM.

Carex nigricans **C. A. Mey.** Infrequent; moist and wet meadows, moist ledge, shrub tundra, and rivulet. A/NAA.

Carex nova **Bailey.** Infrequent; moist meadow, moist ledge, shrub tundra, and rivulet. BM/WNA.

Carex phaeocephala **Piper.** Common; dry and moist meadows, fellfield, dry and moist ledges, krummholz, talus, rock debris habitats, and disturbed area. A/WNA.

Carex praeceptorum **Mackenzie.** Very rare; wet meadow. A/WNA.

Carex pseudoscirpoidea **Rydb.** Very rare; shrub tundra. A/WNA.

Carex pyrenaica **Wallenb.** Infrequent; moist meadow, fellfield, and talus. A/C.

Carex scopulorum **Holm.** Very rare; moist meadow. A/WNA.

Eleocharis acicularis **(L.) Roemer & Schultes.** Very rare; wet meadow. AA/C.

Kobresia myosuroides **(Vill.) Fiori & Paol.** Rare; dry meadow and dry ledge. AA/C.

Juncaceae

Juncus drummondii **E. Mey.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, rivulet, and disturbed area. A/WNA.

Juncus mertensianus **Bong.** Infrequent; moist and wet meadows, moist ledge, shrub tundra, rivulet, and disturbed area. A/NAA.

Juncus tracyi **Rydb.** Very rare; disturbed area. M/WNA.

Luzula spicata **(L.) DC.** Ubiquitous; dry and moist meadows, fellfield, dry and moist ledges, shrub tundra, talus, patterned ground, and disturbed area. A/RM.

Liliaceae

Erythronium grandiflorum **Pursh var. *chrysandrum* (Applegate) Scroggan.** Common; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, talus, and rivulet. M/RM.

Lloydia serotina **(L.) Salisb. ex Reichenb.** Rare; dry meadow and dry ledge. AA/C.

Zigadenus elegans **Pursh.** Infrequent; dry and moist meadows, dry and moist ledges, shrub tundra, and rivulet. AA/NA.

Poaceae

Agropyron scribneri **Vasey.** Infrequent; dry meadow, fellfield, dry ledge, krummholz, talus, and disturbed area. A/WNA.

Agropyron trachycaulum **(Link) Malte ex H. F. Lewis var. *latiglume* (Scribn. & Smith) Beetle.** Common; dry and moist meadows, fellfield, shrub tundra, talus, rock debris habitats, and disturbed area. AA/NA.

Agrostis scabra **Willd.** Very rare; dry meadow. BM/NA.

Calamagrostis purpurascens **R. Br.** Infrequent; dry and moist meadows, fellfield, dry ledge, and krummholz. AA/NAA.

Danthonia intermedia **Vasey.** Infrequent; dry meadow, fellfield, and dry ledge. BM/NAA.

Deschampsia caespitosa **(L.) Beauv.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, talus, rock debris habitats, rivulet, and disturbed area. BM/C.

Elymus glaucus **Buckl.** Very rare; krummholz. BM/NA.

Festuca brachyphylla **Schultes.** Ubiquitous; dry and moist meadows, fellfield, dry and moist ledges, krummholz, talus, patterned ground, rock debris habitats, and disturbed area. AA/C.

Festuca ovina **L.** Very rare; moist meadow. AA/C.

Phleum alpinum **L.** Common; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, and disturbed area. AA/C.

Poa alpina **L.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, rock debris habitats, snowbank, and disturbed area. AA/C.

Poa arctica **R. Br.** Rare; moist meadow and fellfield. A/RM.

Poa epilis **Scribn.** Infrequent; dry and moist meadows, dry ledge, shrub tundra, and krummholz. BM/WNA.

Poa fendleriana **(Steud.) Vasey.** Infrequent; dry and moist meadows, krummholz, and disturbed area. BM/NA.

Poa leptocoma **Trin.** Infrequent; moist meadow, dry ledge, and disturbed area. A/WNA.

Poa rupicola **Nash ex Rydb.** Common; dry and moist meadows, fellfield, dry ledge, krummholz, patterned ground, and rock debris habitats. A/WNA.

Poa sandbergii **Vasey.** Very rare; dry meadow. BM/NA.

Stipa lettermanii **Vasey.** Very rare; dry meadow. M/RM.

Trisetum spicatum **(L.) Richter.** Ubiquitous; dry, moist, and wet meadows, fellfield, dry and moist ledges, shrub tundra, krummholz, talus, patterned ground, rock debris habitats, and disturbed area. AA/C.

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DOUGLAS-FIR DWARF MISTLETOE PARASITIZING PACIFIC SILVER FIR IN NORTHERN CALIFORNIA

Robert L. Mathiasen[1] and Larry Loftis[2]

ABSTRACT.—Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) was found parasitizing Pacific silver fir (*Abies amabilis*) in northern Siskiyou County, California. This is the first report of Douglas-fir dwarf mistletoe on this host. Approximately 40% of the Pacific silver firs near heavily infected Douglas-firs were infected. The low level of infection on Pacific silver fir, unusually large swellings at the points of infection, and poor shoot production on infected branches indicate some degree of host-parasite incompatibility.

Douglas-fir dwarf mistletoe (*Arceuthobium douglasii* Engelm.) is a damaging parasite of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) in the western United States (Graham 1961, Hawksworth and Wiens 1972). Douglas-fir dwarf mistletoe has been reported to occasionally or rarely parasitize true firs (*Abies* spp.), including grand fir (*Abies grandis* [Dougl.] Lindl.), corkbark fir (*A. lasiocarpa* var. *arizonica* [Merriam] Lemm.), subalpine fir (*A. lasiocarpa* var. *lasiocarpa* [Hook.] Nutt.), and white fir (*A. concolor* [Gord & Glend.] Lindl.) (Hawksworth and Wiens 1972, Mathiasen 1984, Mathiasen and Hawksworth 1983). This is the first report of Douglas-fir dwarf mistletoe on Pacific silver fir (*A. amabilis* [Dougl.] Forbes).

Pacific silver fir is a common tree in the Olympic and Cascade mountains of the Pacific Northwest. However, south of Crater Lake, Oregon, it occurs only in isolated populations in Siskiyou County, California (Griffin and Critchfield 1976). We discovered Douglas-fir dwarf mistletoe parasiting Pacific silver fir in one of these populations, approximately 0.5 mile N of White Mountain (T18N, R3W, S31). The infestation of Douglas-fir dwarf mistletoe on Pacific silver fir was about five acres in size at an elevation between 1,580 and 1,700 m (5,200 and 5,600 ft).

The infected Pacific silver firs were in a stand primarily composed of Douglas-fir, white fir, Shasta red fir (*Abies magnifica* var. *shastensis* Lemm.), and western white pine (*Pinus monticola* Dougl.). Infected Pacific silver firs were in the vicinity of large Douglas-firs heavily infected with Douglas-fir dwarf mistletoe. Two other dwarf mistletoes were also present in the stand. Sugar pine dwarf mistletoe (*Arceuthobium californicum* Hawksw. & Wiens) was parasitizing western white pine, and red fir dwarf mistletoe (*A. abietinum* f. sp. *magnificae* Hawksw. & Wiens) was parasitizing Shasta red fir. Confirmation that the mistletoe on Pacific silver fir was Douglas-fir dwarf mistletoe was made by examination of the aerial shoots produced on infected Pacific silver firs. Although only a few shoots were found on infected Pacific silver fir branches, they could be identified as those of Douglas-fir dwarf mistletoe. The shoots of Douglas-fir mistletoe can be distinguished from those of sugar pine dwarf mistletoe and red fir dwarf mistletoe by their small size (Hawksworth and Wiens 1972). Specimens of Douglas-fir dwarf mistletoe on Pacific silver fir have been deposited at the U.S. Forest Service Forest Pathology Herbarium, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Hawksworth and Wiens (1972) devised a 5-class host susceptibility system based on the percentage of infection of potential hosts within 20 feet of heavily infected principal hosts of a dwarf mistletoe. Their system included the following susceptibility classes: Principal (90–100% infection), Secondary (50–89% infection), Occasional (5–49% infection), Rare (more than 0%, but less than 5% infection), and Immune (no infection). To ascertain the susceptibility class of Pacific silver fir to Douglas-fir dwarf mistletoe, we placed circular plots (radius 25 ft) around two large, heavily infected Douglas-firs. Trees within each plot were examined for dwarf mistletoe and the following data recorded for each tree: species, diameter breast height (nearest 2.0 in), and dwarf mistletoe rating (Hawksworth 1977). A total of 46 Pacific silver firs were examined in the two plots and 18 (39%) were infected. This level of infection indicates that Pacific silver fir should be classified as an occasional host for Douglas-fir dwarf mistletoe based on the susceptibility system of Hawksworth and Wiens. The 18 infected trees were distributed by infection class as follows: Class 1 (10), Class 2 (3), Class 3 (2), Class 4 (2), Class 5 (1). Most of the infected Pacific silver firs (72%) had light levels of infection (dwarf mistletoe ratings of 1 or 2). In addition, the presence of unusually large swellings at infection points and poor production of aerial shoots on infected branches indicate a somewhat incompatible host-parasite relationship between Pacific silver fir and Douglas-fir dwarf mistletoe (Hawksworth and Wiens 1972). Although Pacific silver fir is an occasional host of Douglas-fir dwarf mistletoe in northern California, this host-parasite combination is probably not common because Douglas-fir dwarf mistletoe does not frequently occur within the geographic range of Pacific silver fir (Hawksworth and Wiens 1972).

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A DISJUNCT PONDEROSA PINE STAND IN SOUTHEASTERN OREGON[1]

Arthur McKee[2] and Donald Knutson[3]

Abstract.—An isolated stand of ponderosa pine (*Pinus ponderosa*) is surviving on an extremely harsh site in southeastern Oregon. Seed production is low because of insects, primarily pine coneworm (*Dioryctria auranticella*), feeding in developing cones. Seedling establishment is infrequent and difficult because of drought and coarse, rocky soils. A rock-mulch soil surface probably reduces interspecific competition. Because stand size is small (< 2 ha, 57 individuals in 1977) and genetic variability is therefore limited, individual differences in diameter growth are probably due to microsite differences. Mycorrhizae, which could aid tree survival, were absent from a small sample of surface roots. Although the stand was enlarging in 1977, the site is sufficiently severe that local extinction is a possibility.

Isolated populations of a species are of interest to biologists because such populations frequently represent unique genotypes adapted to particular habitats. In September 1975 and March 1977, we visited a disjunct stand of ponderosa pine (*Pinus ponderosa*) previously reported by Packard (1970). The isolation of the stand, 105 km from the nearest ponderosa pine (Fig. 1), and the reported old age (± 300 years) of a few of its trees (Packard 1970) suggest the possibility of novel ecological relationships or adaptations for extreme drought. In this paper, we describe the status of the stand in 1977, discuss its development, and report changes in diameter growth rates over the past two centuries.

Site and Stand Description

The disjunct stand, located in Malheur County, Oregon, 14.5 km WSW of Rockville (T26S, R45E, Sec. 30, W1/2), occurs on a steep, bare ridge of rhyolitic tuff at approximately 1,450 m elevation. The ponderosa pine are growing along the crest of the ridge

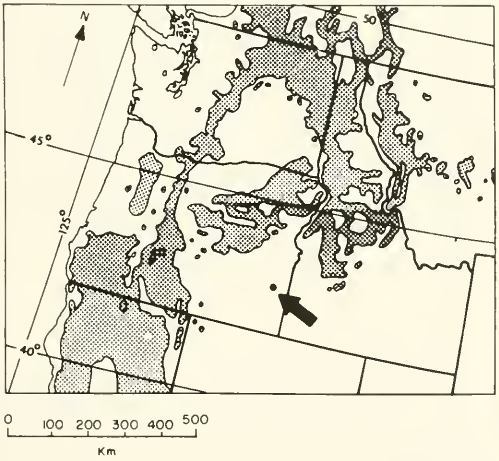

Fig. 1. Distribution of ponderosa pine (shaded area) in the Pacific Northwest. Arrow shows location of the disjunct pine stand (adapted from Little 1971).

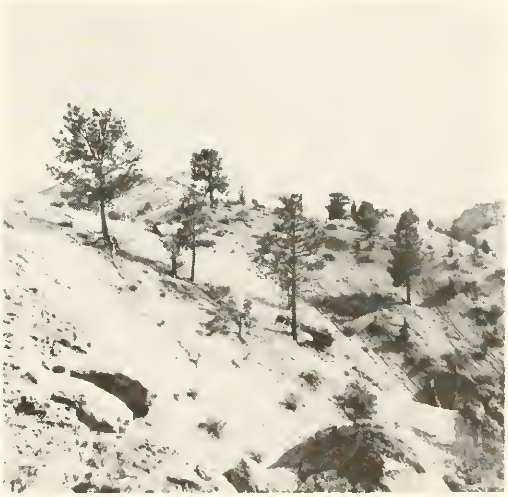

Fig. 2. Site overview showing the ridge-top position of the disjunct stand, the rocky mulch nature of the soil surface, and the absence of litter. Tree farthest left is the oldest (as of 1977: 415 years, 14.5 m tall, 75.5 cm dbh).

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TABLE 1. Soil characteristics of the disjunct ponderosa pine stand compared with those of other sites dominated by sagebrush (*Artemisia* spp.) stands in eastern Oregon.

	Disjunct pine stand[a]		Other sites[b]			
			1	2	3	4
County	Malheur		Malheur	Malheur	Baker	Union
Township, range, section	26S,45E,30		17S,43E,12	14S,39E,28	6S,39E,2	8S,41E,18
Soil depth (cm)	0–5	5–15	0–15	0–15	0–15	0–15
Soil pH	6.01	5.65	7.7	7.6	7.6	7.6
Organic matter (%)	0.44	0.42	0.8	1.2	1.2	1.5
Cation exchange capacity (meq/100 g soil)	8.7	7.7	23.8	24.5	34.1	36.7
Extractable cations (meq/100 g soil)						
Calcium	4.9	4.6	15.2	18.0	26.2	29.0
Magnesium	2.1	2.1	5.9	6.4	11.4	12.9
Sodium	0.06	0.06	1.9	1.3	8.2	6.8
Potassium	0.17	0.11	2.2	1.2	1.4	1.6
Kjeldahl nitrogen (%)	0.033	0.027	0.07	0.1	0.05	0.07
Total phosphorus (ppm)	11.0	18.0	10.6	8.5	10.6	5.6

[a] Soil values for the disjunct stand are means of three samples.
[b] Courtesy Oregon State University Soil Characterization Laboratory, Corvallis.

and on the upper portions of the steep northeast and southwest slopes (Fig. 2). The soil surface is covered by a loose, rocky mulch. Soil 0–15 cm deep is slightly acid (mean pH 5.8) with very low carbon content (0.44%) and cation exchange capacity (8.2 meq/100 g soil) (Table 1). Levels of calcium, magnesium, sodium, and potassium are also low, more comparable to levels in humid than semiarid cold, temperate regions (Brady 1974). Although nitrogen levels are low (0.03%), the carbon:nitrogen ratio (15:1) is comparable to that in agricultural soils. Few plants other than ponderosa pine are growing on the site (Fig. 2). Shrub cover is especially sparse compared with that of the surrounding area, which is dominated by big sagebrush (*Artemisia tridentata*) and low sagebrush (*A. arbuscula*) with widely scattered juniper (*Juniperus occidentalis*).

The entire stand covered < 2 ha and contained 57 individuals in 1977. Forty-nine trees were < 25 years old (Table 2). Several seedlings appeared to be < 5 years old, as determined by number of branch whorls and terminal bud scars; five trees were between 26 and 100 years old; and three trees were over 100 years old, the two oldest of which had 415 and 232 annual growth rings at stump height. The largest individual was 75.5 cm in diameter at breast height (dbh) and 14.5 m tall, and only two others were over 40 cm dbh and 9 m tall.

TAXONOMIC CHARACTERISTICS

More than 50 needle fascicles from each of 10 trees were examined, and only three-needled fascicles were found. Needles averaged 20 cm long (range: 18–21 cm), which is midrange for ponderosa pine (Mirov 1967); they were dark green and generally appeared to be healthy. Both mature and immature cones were examined from several trees. Mature cones were quite short, averaging 8.1 cm long (range 6–10 cm); immature first-year cones averaged 5.5 cm long. Slightly recurved prickles, rather than the more common straight prickles, were observed, a trait often found on ponderosa pine cones in eastern Oregon.

DISCUSSION

The site clearly is harsh for ponderosa pine, as evidenced by short stature and slow growth of the older trees. Flat-topped crowns show multiple leaders, with none achieving apical dominance (Fig. 2).

Seedling establishment has been infrequent and episodic. Five trees became established near the turn of this century, about 30 trees in the early 1950s, and about 10 trees in the early 1970s. These periods of establishment also were periods of relatively fast diameter growth for the two largest trees (Fig. 3), probably indicating a more favorable cli-

Table 2. Number of individuals, by diameter, height, and age classes, in the disjunct ponderosa pine stand.

Diameter (cm)	Height (m)							
	0.5	0.6–1.5	1.6–3.0	3.1–4.5	4.6–6.0	6.1–7.5	7.6–9.0	9.0+
	< 25 years old			26–100 years old			101+ years old	
0–10	32	12	5					
11–20				1	1	1		
21–30							1	
31–40							1	
41–50								2
51–60								
61–70								
71–80								1

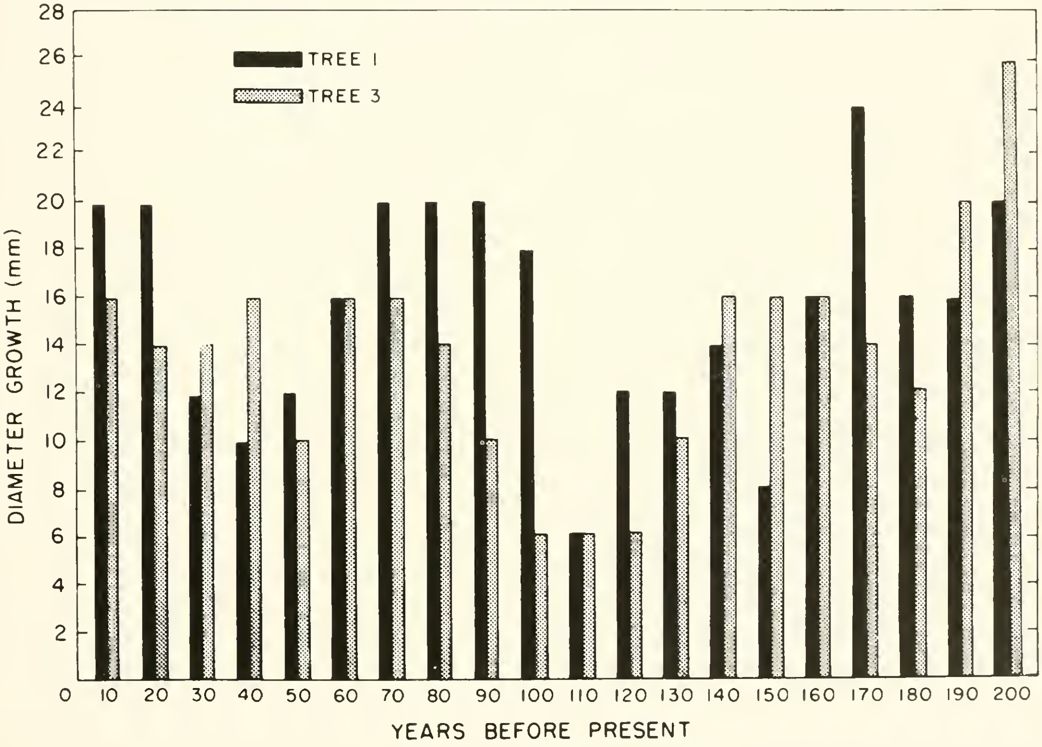

Fig. 3. Patterns of diameter growth, per decade, of the two oldest trees in the disjunct stand (as of 1977: tree #1, 415 years; tree #3, 232 years).

mate. For most of the past 200 years, however, diameter growth has been very slow, with the slowest periods 50 and 110 years ago. The droughty conditions that restrain diameter growth would likely restrict seed germination and establishment of young seedlings as well.

Seedbed conditions also influence establishment. The rocky mulch covering the steep slopes is unstable enough to be moved by frost, wind, and animals; such movement would tend to bury those seedlings managing to get a taproot into the soil. Perhaps more important, the rocky mulch may also reduce interspecific competition by preventing invasion of the site by other plant species. Ponderosa pine has, by far, the largest seeds of any of the local species. A large seed with

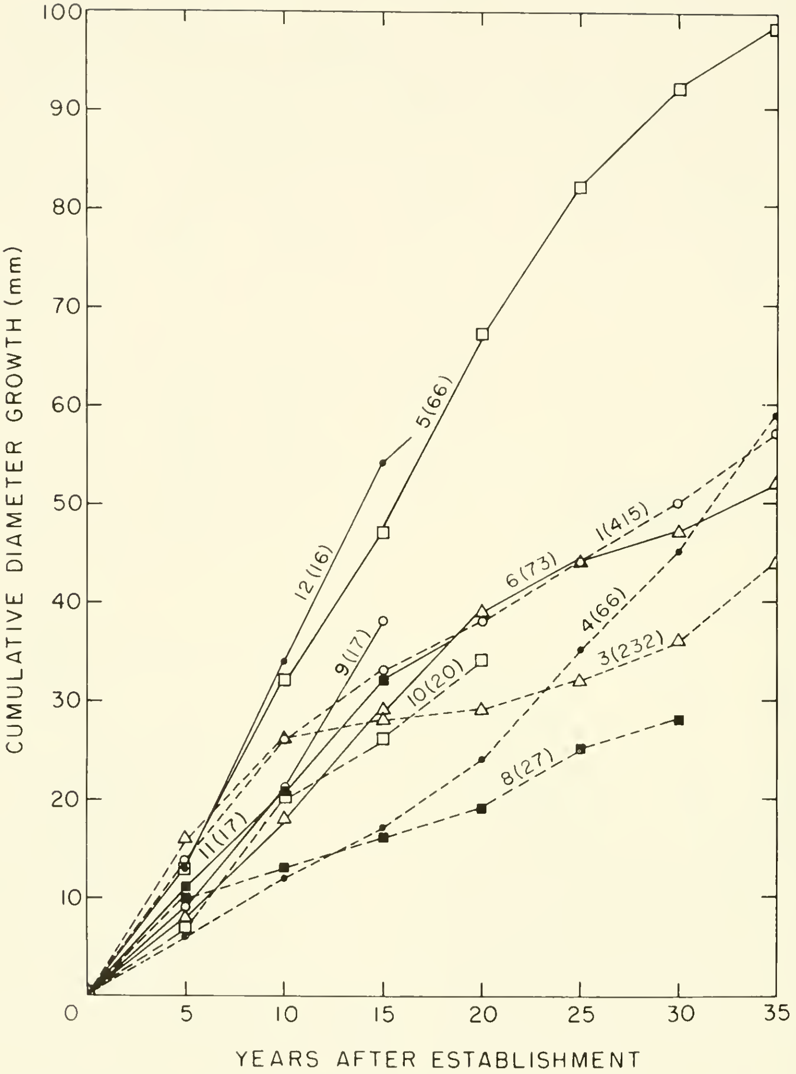

Fig. 4. Cumulative diameter growth of 10 of the largest trees in the disjunct stand (tree number is shown on the line, number of growth rings at stump height in parentheses).

substantial energy reserves may be just what is needed to germinate and rise through the rock mulch. This stand may, in fact, owe its existence to the presence of the rocky mulch despite the difficulties it presents for seedling establishment.

In addition to the harsh climate, insects feeding on seeds seem an important factor regulating establishment. In fall 1975, 15 trees had mature cones, and all were damaged by the pine coneworm (*Dioryctria auranticella*) probably surviving in nearby juniper trees; immature cones were similarly damaged. The same degree of insect damage was observed in spring 1977. If this degree of annual seed predation is typical, then very few sound seeds are available for germination in any given year. This same insect also attacks twigs and shoots (Furniss and Carolin 1977) and might account for the multiple leaders observed in the older trees.

Despite the presence of a fire scar at the base of the oldest tree, fire probably has not been a major factor in stand development because of the lack of on-site fuel (Fig. 2).

We have no explanation for the origin of the stand; perhaps the seeds were carried by Indians or were dispersed by animals. It may be a remnant of ponderosa pine stands existing in the area thousands of years ago when the climate was more favorable. We have no evidence that this is, in fact, a relict stand. There is also no evidence—such as standing dead or downed trees—that the stand has been more extensive in the last century or two. At one time, the population may have consisted of two or perhaps even one individual. Once a tree was established, the general trend was for slow and relatively linear diameter growth during the first three decades (Fig. 4). The data show that variation is as great within a cohort as between. Cumulative diameter growth of trees 4, 5, and 6, all in the same cohort, shows a wide range, which could be due to genetic or microsite differences. Limited cross-pollination in this very small population would have greatly reduced genetic variability; therefore, variations in growth are probably the result of variations in microsite conditions.

Particular mycorrhizal fungi can enhance the survival of their coniferous symbionts. *Cenococcum geophilum* and *Pisolithus tinctorius* both form mycorrhizal associations on droughty sites (Trappe 1977). However, no mycorrhizae were found in small roots near the soil surface nor were any mushrooms present in the area. Because ponderosa pine has a deep taproot, extensive excavation would be necessary to thoroughly evaluate the presence and identity of mycorrhizal fungi.

The survival of this stand is uncertain. The large number of seedlings relative to the number of mature trees indicates a new period of stand enlargement. The site is sufficiently harsh, however, and the population so small as to make local extinction a serious possibility.

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NOTES ON AMERICAN *SITONA* (COLEOPTERA: CURCULIONIDAE), WITH THREE NEW SPECIES

Vasco M. Tanner[1]

ABSTRACT.—Historical notes extracted from a taxonomic revision of American representatives of *Sitona* Germar are presented. Described as new to science are *Sitona alpinensis* (Utah to Northwest Territories), *bryanti* (Arizona), and *oregonensis* (Oregon to Washington).

Preface

The author (now 94 years of age) commenced a taxonomic revision of the weevil genus *Sitona* in 1954 and labored with it until January 1977 when advancing age prevented finalization of the manuscript. Because of the great effort he expended on this project, the family has requested that the introductory pages and the descriptions of new species be published as his final contribution to science in the journal he founded. Although some of the terminology is outdated, the introduction and descriptions are presented as he wrote them. The paratypes of *alpinensis* and *oregonensis* were distributed more than a decade ago; it is presumed that those not accounted for here are mostly in the U.S. National Museum and in the British Museum (Natural History). Treated in the unfinished manuscript are 23 species; 4 are introduced from Europe, and 19 are regarded as native to America. A review of the full text of the manuscript is in progress.—Editor.

INTRODUCTION

The genus *Sitona* is rather large, containing between 90 and 100 valid species from the Palearctic and Nearctic regions. Casey (1888) described 16 species from the western United States, 10 of which are considered as valid species in this study.

A total of 23 species are dealt with in this treatise; four are introduced species. Sixteen native species were previously described, and three new species are proposed.

The weevil species assigned to the genus *Sitona* by Casey have been for many decades in a nebulous taxonomic state. Thomas L. Casey, the son of Brig. Gen. Thomas Lincoln Casey, graduated from the United States Military Academy at West Point in 1879 and was admitted to the Corps of Engineers. He remained in the military service until his retirement in 1912, having reached the rank of colonel. For three years, 1885–87, Casey's official military duties called him to the Pacific Coast. "During this time, many portions of California, Nevada, Arizona, and portions of Texas were explored by himself in person" (Casey 1888:229). While in California, Casey and several other entomologists in California collected about 3,500 specimens of Coleoptera which he transported to his quarters when he returned to Washington, D.C.

Casey's (1888) treatise, Sitoninae, was based largely upon specimens of *Sitona* he accumulated while stationed in California. He devoted much of his life to acquiring and studying the Coleoptera of America. He died in February 1925.

He bequeathed his notable entomological collection to the United States National Museum. "In order to assure the perpetuity of this valuable collection, Col. Casey's wife, Mrs. Laura Welsh Casey, established a memorial fund to provide for the care and knowledgeable curatorial work in the handling and installation of the collection" (Buchanan 1935).

The collection consisted of "12,245 named forms with a total of 116,738 specimens and more than 9,200 holotypes" (Buchanan 1935). L. L. Buchanan was appointed to serve as curator. "The curatorial work was started by Mr. Buchanan on 1 April 1926, and was continued half a day at a time, for a period of 5 years" (Buchanan 1935).

Buchanan was meticulous in transferring the Casey specimens. "The cardinal rule guiding the curatorial work was to preserve exactly Casey's concept of each species. Regardless of occasional conflict with accepted synonyms,

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[1] Formerly at Life Science Museum, Brigham Young University, Provo, Utah 84602.

Casey's arrangement of specimens was strictly followed; furthermore, steps were taken to virtually guarantee the permanent preservation of this arrangement, so that students, both now and in the future, will have equal assurance that before them stand Casey's actual original series of each species; and not a hodge-podge resulting from accidental misplacement of specimens or interpolation of later and irrelevant material" (Buchanan 1935:6).

I have greatly appreciated the care and accuracy exercised by Buchanan as he transferred the specimens into the museum collection. During the course of this study, I had the opportunity of visiting the museum on nine different occasions and studying the species of *Sitona* as Casey had arranged them. I always found Buchanan and his aide and successor, Dr. Rose Ella Warner, very cooperative and helpful.

In the 1888 study in which Casey described 16 new native species of *Sitona*, he did not recognize Say's species *Sitona indifferens* and *S. scissifrons* or the two distinctive species *S. californicus* Fahraeus and *S. vittatus* LeConte, nor did he consider to any extent the variability in size, color, and color pattern of the species he treated.

In 1831, Say (LeConte 1859) discussed 135 species of American weevils, 95 of which he described as new species, including *Sitona indifferens* and *S. scissifrons*, both inhabitants of Missouri. His description of *S. scissifrons* is brief, but it is more accurate and complete than that of *S. indifferens.*

Because the original type series of *S. scissifrons* was destroyed, and because it is now established that only one good native American species inhabits Missouri, in order to fix the identity of *S. scissifrons*, I have designated a specimen collected at Rock Port, Missouri, by R. E. Munson as the Neotype. This Neotype was deposited in the Entomological Collection at the U.S. National Museum, Washington, D.C.

The type specimens of LeConte's *Sitona sordidus* and *S. vittatus* were loaned to me. These have been studied in connection with a large series of specimens from California.

The validation of *Sitona californica* Fahraeus has been considered in some detail in the treatment of this species in the main text of this study.

History

The genus *Sitona* was proposed by Germar (1817) and was subsequently cited by Germar (date ?), Schoenherr (1826, 1834), and Say (1831). Schoenherr (1840) changed the spelling to *Sitones* from which time it had rather wide usage (LeConte and Horn 1876, Casey 1888). Germar's *Sitona* has priority over Schoenherr's *Sitones.*

Sitona is the sole genus of the tribe Sitonini, subfamily Thylacitinae (Kissenger 1964). It is distinguished from all other tribes by the punctation and pubescence of the mandibles, which are sharp and without a tooth on their internal edge and curved into a hook at the apex. Some 90 to 100 species are widespread in the Nearctic and Palearctic regions. Some of the useful characters for distinguishing this genus have been listed by the following authors of *Sitona:*

"*Character generis:* Antennae breviusculae, subtenues; articulis primis funiculi longiusculis, obconicis, reliquis nodosis; clava oblongovalis; rostrum supra planum aut in medio linea impressum, aut sulcatum; occuli majusculi, in plerisque subrotundati, modice prominuli, in nonnullis oblongi, valde prominuli; thorax subteres, lateribus pone madium rotundatus; elytra elongata, apice rotundata; humeri obtuse angulati" (Schoenherr 1826:134).

"Antennae geniculate, rather short and slender; the scape elongation clavate, reaching to the middle of the eyes; funiculus with the first and second joints rather long, obconic; the remainder nodose; club elongate-ovate, acuminate. Rostrum short nearly horizontal; the apex emarginate, above flat, with an impressed longitudinal line or groove; eyes rather large, sometimes rounded, moderately prominent, or oblong and very prominent. Thorax rounded, with the sides a little dilated beyond the middle, as dilated in the middle; scutellum minute, rounded; elytra elongate, with the apex rounded, the shoulders obtusely angulated; legs moderate; femora incrassated in the middle; tibiae truncate at the apex, unarmed" (Stephens 1831:132).

"Mandibles lacking scar, punctured, and with pubescence" (Fowler 1891:216).

"Antennal grooves deep, short, curving abruptly downwards just behind the antennae, scape reaching middle of eyes, funicle

7-jointed, joints 1 and 2 thick, 3–7 shorter, club elongate, ringed eyes prominent, round to oblong; front coxae contiguous, hind ones widely separated; claws slender, divergent, appendiculate" (Blatchley and Leng 1916: 140).

"Scape shorter than breadth of head including eyes" (Joy 1932:176).

"*Sitona* normally lacks the mandibular scar in the adult and its larva has spiracles with paired annulate air tubes" (Crowson 1955: 165).

"Rostrum broad and short, and with impressed median line; head behind eyes not much broader than base of rostrum" (Kevan 1959:251, 259).

"Tarsal claw with auxiliary clawlike seta" (Kissenger 1964:23).

In this study the male genitalia have proven to be of value in separating the species; female genital structures are poorly developed and of little, if any, value in the classification of species in this genus.

The above characterizations of *Sitona* help to identify this genus. The following are some of the major characteristics which have helped to separate the species of *Sitona:* (1) Inner margin of eye not prominent; inner margin of eye prominent; (2) prothorax with distinct median vitta; prothorax without distinct median vitta; (3) elytra without erect setae; elytra with erect setae; (4) thorax finely punctured; thorax deeply punctured; (5) beak and front sulcate; beak and front not sulcate; (6) aedeagus with pointed median lobe; aedeagus with angular median lobe; (7) size of species specimen (a) small or (b) large; (8) elytra tessellate or not tessellate.

Specimens of a species will fall into one or the other of the above couplets but will also be distinctive in a number of other characteristics. These extrinsic and intrinsic characters within a species, which will affect the color, color pattern, size, and shape of individuals, color and density of body scales, and bodily structures will then need to be carefully studied and recorded. In this study much time has been spent checking type specimens of the Casey Collection with many specimens from type areas. This has necessitated the synonymizing of a number of Casey's species. As early as 1886, Casey disclosed that the only specimen with which he was concerned was the specimen he described. "It will be observed that the descriptions refer in all cases to the single specimen assumed as the type"; and "I have preferred, therefore, in the existing state of knowledge, to describe one definite type and give such general remarks as may indicate the variation exhibited by the material at hand" (Casey 1886).

My study of the Casey Collection of *Sitona* specimens, the comments made by Buchanan, and the observation by R. E. Blackwelder (1950) that "on the average, nearly half of the species named in the collection were described by Casey and consist of a holotype and sometimes a few paratypes," have convinced me that if Casey, as he described the above-mentioned native species, had been provided with more specimens for his study and had noted the extent of variation upon which to base each of his new species, the treatise of the *Sitona* in 1888 would have been much improved.

An examination of Casey's *Sitona* specimens revealed that he had very few specimens of most of the species he described. His *Sitona* paper and the U.S. National Museum catalog accession record of the type specimens of *Sitona*, transferred from the Casey Collection by Buchanan in April 1927, show the following were represented: *extrusus* 3, type (2 paratypes missing) +1 ex. Colo.; *varians* 13, type; *margaritarus* 2, type (paratype missing); *procerus* 1, type; *occidentalis* 2, type (+1 paratype); *eximius* 4, type (+3 paratypes); *montanus* 2, type (+1 paratype); *nebulosus* 1, type; *alternans* 1, type; *osculans* 2, type (paratype missing); *prominens* 2, type (+4 ex.); *hispidiceps* 2, type (1 paratype +6 ex.); *augustulus* 1, type (+1 ex.); *explicitus* 1, type (+10 ex.); *apacheanus* 2, type (paratype missing); *sparsus* 1, type.

NEW TAXA

Sitona alpinensis, n. sp.

Fig. 1

Derm black, scales small, some round, elongate, dense, colored white, brown, black, some iridescent; setae short, black and white, obscurely interspersed among the scales. *Head* as long as rostrum, wider at base than rostrum; interocular space as wide as length of head, occiput punctate, concealed by scales and setae. Eyes large, slightly ovate, some scales, but no long setae over the dorsal inner

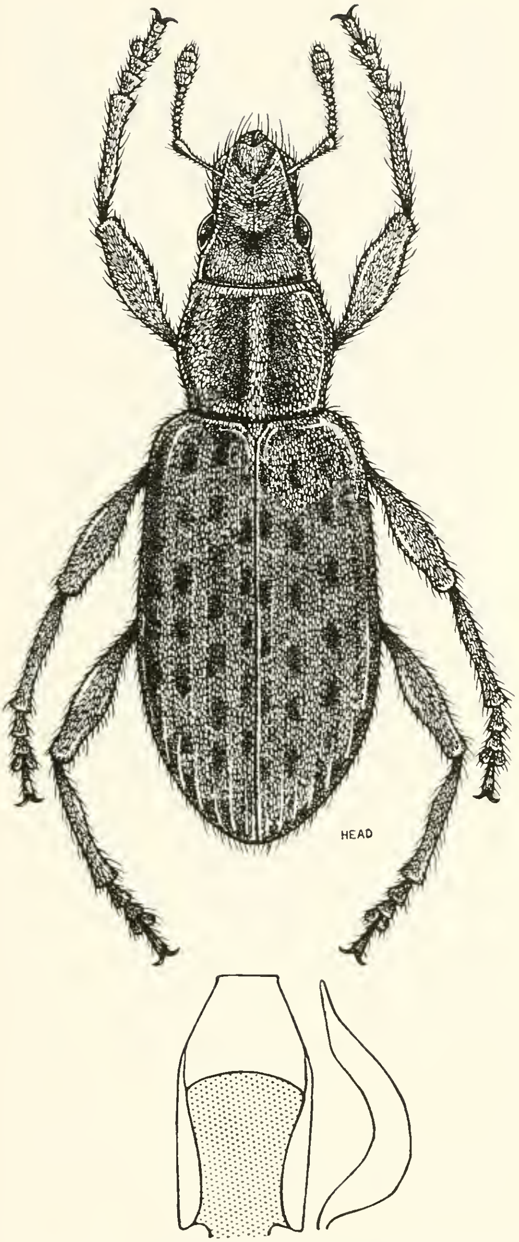

Fig. 1. *Sitona alpinensis:* dorsal aspect of adult, dorsal and lateral aspects of median lobe of male genitalia.

margin of eye. Rostrum concave, sulcus deep, extends from fovea between eyes to apical flattish area of rostrum. Antenna reddish brown; scape extending to middle of eye; first joint of funicle longer than second; second as long as segments 3–4 combined; club as long as segments 4–7 combined; scrobes deep, directed downward, areas covered with scales between posterior margin of scrobe and anterior margin of eye. *Prothorax* convex, densely covered with scales and decumbent setae; widest before the middle, wider than long, constricted and slightly elevated at apex; base and apex truncate; punctures deep and numerous, lateral and medial vitta of white scales and setae; scutellum with white setae. *Elytra* twice as long as wide, sides parallel two-thirds of length, greatest convexity near declivity, costate, striae punctured, extending from base to apex of elytra; with humeral carina; scales small, vitta of white ones extending posteriorly, sutural area with brown scales, some blotches of black scales in declivitous area; apex rounded, moderately acuminate. Legs, posterior femora extending to posterior margin of fourth ventrite; clothed with white decumbent setae, club of femora moderate in size with a few small white scales; prosternal coxal cavities open. Ventrites 1–2 about equal in width, 3–4 shorter and equal in width, segment 5 as wide as 3–4 combined; all segments clothed throughout with white setae and scales. Pro-, meso-, and metasternites uniformly clad with white setae and few scales.

LENGTH: 5.2–7.1 mm; breadth: 2.3–2.9 mm.

TYPE LOCALITY: Holotype, Glacier Lake (Emerald Lake), Mount Timpanogos, Utah County, Utah, elevation 10,000 feet; July 1941 (Vasco M. Tanner); allotype, same data as holotype; 20 paratypes: 7, Glacier Lake (Emerald Lake), Mount Timpanogos, elevation 9,800 feet (L. F. Braithwaite, S. K. Taylor, and V. M. Tanner); 3, Hidden Lake, Mount Timpanogos, Utah County, Utah, elevation 9,700 feet, 27 July 1940 (C. L. Hayward); 3, Aspen Grove, BYU campus environs, Mount Timpanogos, Utah County, Utah, elevation about 6,500 feet (Lowell Miller, V. M. Tanner); 1, Bear Paw Mt., Montana, September 28 (Hubbard and Schwarz); 1, Helena, Montana (collection of C. W. Leng); 1, Gallatin Val., Montana, 10 July 1907 (Wickham Collection, 1933); 1, Gallatin County, Montana, elevation 9,400 feet, 10 July 1900 (E. Koch); 1, Good Hope, N.W.T., 20 June 1931, Lot 237 (Owen Bryant), found on dwarf pea, *Astragalus* sp.; 1, Yukon Crossing, Y.T., Can. 24, Vol. 11 (J. M. Jossup).

The holotype, allotype, and one paratype are in the Life Science Museum, Brigham Young University. The remaining paratypes were distributed more than a decade ago, but no record was kept of where they were sent.

CHARACTERISTICS: *Sitona alpinensis* is related to *S. cylindricollis* Fabricius in body shape and color of scales, but *alpinensis* is a larger species, the rostrum concave, sulcus deep, extending from fovea between eyes to apical flattish area of rostrum. Eyes are large and prominent. Elytra with well-developed costae at least on odd-numbered interstriae. The genitalia of *alpinensis* are distinctive. The median lobe is broader, shorter, and with two orificial plates. *Sitona alpinensis* is a high-altitude form, having been collected only in the Hudsonian and subalpine zones.

Sitona bryanti, n. sp.

Fig. 2.

Form robust, derm black; scales and setae black, except white scales on medial vitta of prothorax and lateral vittae of elytra; white scales and setae on ventrites and legs. *Head* longer and wider than rostrum; sulcus prominent, deep, extending from fovea between the eyes to carina of the rostral disc; frontal of head between eyes flat; eyes prominent, elongated, two-thirds as long as the head; inner margin slightly elevated above margin of head; deep punctures on head and rostrum; long black and silvery setae on the rostrum and head; scrobes deep and discernible from above; antennae dark rufous; scape of antennae reaching middle of eye; first joint of funicle as long as joints two and three combined; club large, as long as segments 3–7 combined. *Prothorax* slightly wider than long; not constricted at apex; widest at middle, apex and base equal; thickly punctured and covered with black scales and setae, except for a prominent medial vitta of small elongate white scales. *Elytra* three-fourths as wide as long; sides straight and parallel in basal three-fourths, acutely rounded at apex; disc convex, basal area not elevated, surface without striae, middle of disc punctate, closely covered with small elongate black scales and black, decumbent setae; lateral vittae of white scales extending from humeri to umbones; declivitus and covered with white scales and setae from umbones to apex. Legs uniformly brownish in color, clothed with long, decumbent, silvery setae; ventrites with thick, low-lying, whitish scales and setae.

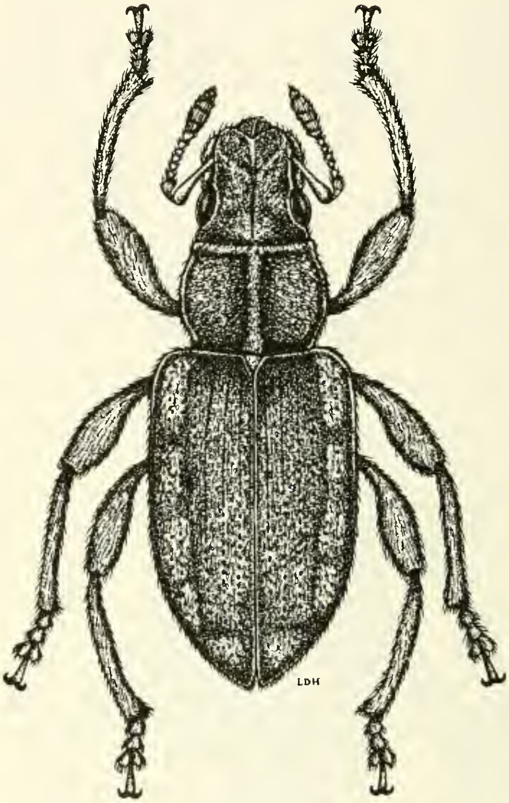

Fig. 2. *Sitona bryanti*: dorsal aspect of adult.

LENGTH: 4 mm; width: 1.5 mm.

TYPE LOCALITY: Flagstaff, Coconino County, Arizona. 3-VIII-1936. Owen Bryant, collector. I take pleasure in naming this species after Owen Bryant who was a very discerning collector. He was a frequent visitor at Brigham Young University and contributed more than 800 specimens of Curculionidae to the entomological collection of the University.

The unique holotype is in the Life Science Museum, Brigham Young University.

Sitona bryanti is a distinctive species. It is small in size, robust in form, with broad, short head and rostrum, medial vitta on prothorax and with lateral vittae on elytra.

Sitona oregonensis, n. sp.

Fig. 3.

Derm black, robust, elongate, scales ovate, dense, white, brown, and black in color; black

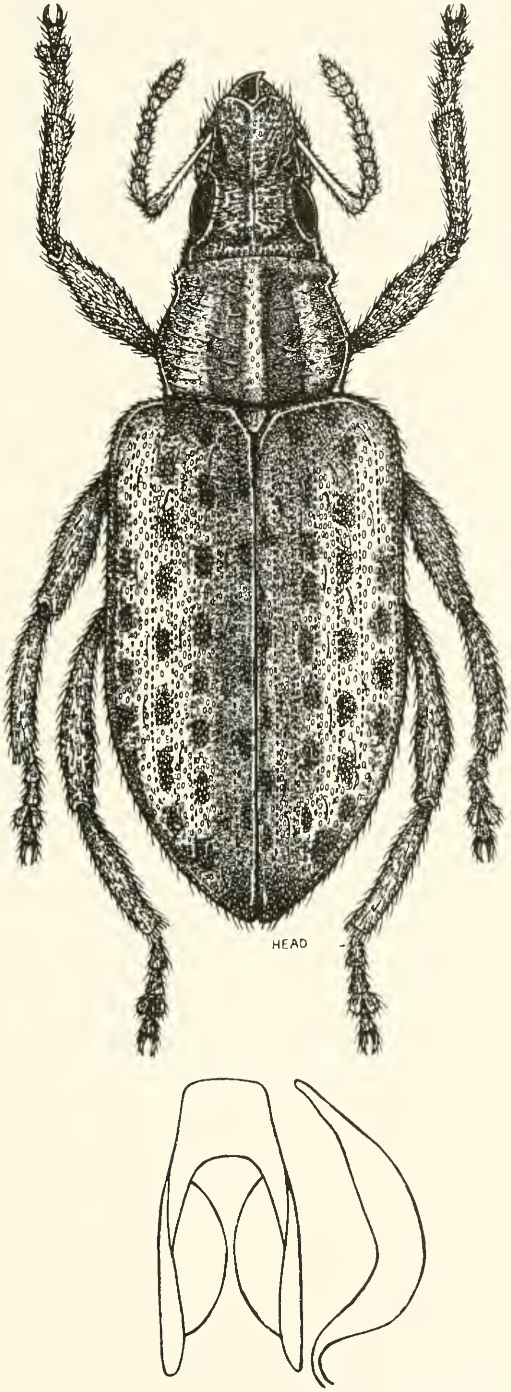

Fig. 3. *Sitona oregonensis:* dorsal aspect of adult, dorsal and lateral aspects of median lobe of male genitalia.

scales in patches along intervals of elytra; scales on ventral segments dense, white, elongate, and intermixed with low-lying setae. *Head* wider than long; head and beak squamose and punctate; few short brown setae bordering the eyes; long white setae on rostrum, intermixed with iridescent scales; space between eyes level, divided by deep sulcus, which extends to central fovea of rostrum; eyes prominent, noticeable, convex, inner margins slightly elevated above margin of head; antennae dark rufous; first joint of funicle as long as joints two and three combined; scrobes deep and discernible from above. *Prothorax* at middle considerably wider than long; elevated in middle, sloping to apex and base; strongly constricted at one-fifth the length from apex on the sides; base feebly constricted, disc convex, sides arcuate surface punctures obscured by covering of elongate scales; trivittate, marginal stripes well developed, median one narrow; base and apex unequal. Scutellum well developed, covered by white scales. *Elytra* three times as long as the prothorax and about twice as long as wide; sides straight and parallel in basal three-fourths, acutely rounded at apex; disc convex; basal sutural area slightly elevated; intervals tessellate with black scales and setae, medial area with dark bands, lateral portions with bands of white scales; umba with black scales; punctation obscured by dense covering of scales and setae; sparse white setae along lateral and posterior area. Legs densely covered with light, decumbent setae, scales sparse; venter clad with dense white scales and low-lying setae.

LENGTH: 5.6–6.1 mm; breadth: 2.6–2.9 mm.

The median lobe of the aedeagus is short, narrowed toward the rounded apex.

HOLOTYPE: Tigard, Washington County, Oregon, 11-V-1944 (Anderson), on leaves of lupine. Allotype: Tigard, Washington County, Oregon, 11-V-1944 (Anderson). Paratypes: 5, Tigard, Washington County, Oregon, 11-V-1944 (Anderson); 5, Cornelius Pass, Washington County, Oregon, 9-IV-1936 (K. Gray and J. Schub); 2, Portland, Multnomah County, Oregon, 8-V-1941 (J. Schuh) on Russell lupine; 1, Longview, Cowlitz County, Washington, 16-IX-1944 (Anderson); 1, Forest Grove, Washington County, Oregon, 8-V-1938 (mech trap); 1, Sleilacomm, Pierce County, Washington, 24-V-1945 (Forsell) on lupine leaves.

The holotype, allotype, and five paratypes are in the Life Science Museum, Brigham Young University. The remaining paratypes were distributed more than a decade ago, but no record was kept of where they were sent.

The robust size of the females, vittate prothorax, tessellate elytra, elongate, broad, parallel sides, and angular apices of the median lobe of the aedeagus are distinctive characteristics of *oregonensis* which distinguish it from related species *californicus*, *prominens*, and *lupina*.

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ECOLOGICAL COMPARISON OF SYMPATRIC POPULATIONS OF SAND LIZARDS (*COPHOSAURUS TEXANUS* AND *CALLISAURUS DRACONOIDES*)

Donald D. Smith[1,2], Philip A. Medica[1,3], and Sherburn R. Sanborn[4]

ABSTRACT.—Sympatric populations of *Cophosaurus texanus* and *Callisaurus draconoides* were periodically sampled from March 1973 through April 1974 at Burro Creek, Mohave County, Arizona. *Callisaurus* were also sampled at Rock Valley, Nye County, Nevada. Sex ratios were skewed in favor of males in the adult *Cophosaurus* but were equal in both adult populations of *Callisaurus*. Both species became sexually mature as yearlings. Mean clutch sizes were 3.55 (±0.83) for *Cophosaurus*, and 4.25 (±1.08) and 5.07 (±1.33) for *Callisaurus* at Burro Creek and Rock Valley respectively. Evidence of multiple clutches was exhibited by both species. Egg weight/body weight ratios for both species and clutch weight/body weight ratios for *Cophosaurus* were notably smaller than previously reported.

At Burro Creek both species were highly insectivorus, with orthopterans comprising the largest food group of each. Niche overlap for food was high at the ordinal level, but at the familial level it is apparent that *Callisaurus* probably fed in the more xeric areas of the riparian habitat.

No differences were found in the temperature responses of these two lizards. However, minor temporal separations and substantial spatial partitioning were observed. *Callisaurus* preferred sandy open areas, while *Cophosaurus* preferred the presence of some rocks and boulders.

Ecological studies of *Callisaurus draconoides* have been conducted by Kay et al. (1970), Pianka and Parker (1972), Tanner and Krogh (1975), and Vitt and Ohmart (1977). Studies of *Cophosaurus texanus* have been done by Johnson (1960), Ballinger et al. (1972), Shrank and Ballinger (1973), Engeling (1972), and Howland (1984). Clarke (1965) studied the ethology of both of these lizards as well as that of *Holbrookia*. Prior to our field work, no comparative ecological study had been done of sympatric populations of *Callisaurus draconoides* and *Cophosaurus texanus*. These two sand lizards are recognized as being closely related (Peters 1951, Clarke 1965) and exhibit geographic distributions that are usually mutually exclusive. It is hoped that this study will provide insights into their descriptive ecological characteristics and some of the interrelationships of these two populations.

In the spring of 1966, P. A. Medica collected a single specimen of *Cophosaurus texanus* near Burro Creek, 32 km S of Wikieup, Mohave County, Arizona. In May 1970, D. D. Smith discovered *C. texanus* near the same locality to be sympatric with *Callisaurus draconoides*. This area is described in Stebbins (1966) as a disjunct locality in the distribution of *Cophosaurus*. Another pair of saurian species not often found to be sympatric were also present at the study site, *Uta stansburiana* and *Urosaurus ornatus*. Other species of reptiles and amphibians observed at the study locality include *Cnemidophorus tigris*, *Sauromalus obesus*, *Sceloporus magis-*

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ter, *Crotalus mitchelli*, *Kinosternon sonorense*, *Bufo microscaphus*, and *Hyla arenicolor*. Additional noteworthy locality records have been recorded for *Thamnophis cyrtopsis* (Smith and Medica 1973), *Eumeces gilberti* (Medica and Vitt 1974), and *Masticophis bilineatus* (Medica and Maza 1974).

METHODS

Between 3 March 1973 and 7 April 1974 nine weekend field trips were taken to Burro Creek (15 km W of Bagdad), Mohave County, Arizona. Field work normally began about 0700 hours (hr) and continued until approximately 1400 hr when most lizard activity had ceased. Then in the evening we sampled lizards again between 1730 hr and sunset. Lizards were collected along either side of Burro Creek and from the water's edge sometimes up the arroyos and onto the surrounding bajadas. Lizards were collected by noosing or by shooting with BB guns or .22-caliber revolvers loaded with #12 shot cartridges.

Each time a lizard was secured, the following data were recorded: cloacal temperature, air temperature at about 2 cm, and soil surface temperature using a Schultheis quick-reading thermometer 20–70 C. The habitat type, soil type, and lizard's activity were also recorded. The animals were then frozen with dry ice and transported to the laboratory for autopsy. From the Burro Creek locality 116 *Cophosaurus texanus* and 132 *Callisaurus draconoides* were removed for analysis. In addition, during the summer of 1973, a parallel sample of 91 *C. draconoides* was collected from Rock Valley, Nye County, Nevada (322 km NW of Burro Creek), to be analyzed similarly to those from Burro Creek for information on reproduction. This was done in an effort to gain insight into latitudinal variation in this species during the same season and to obtain further baseline data for comparison with the well-studied population of Frenchman Flat reported by Tanner and Krogh (1975). All specimens have been deposited at the Los Angeles County Museum of Natural History, Section of Herpetology.

In the laboratory, snout-vent (s-v) and tail lengths were measured to the nearest mm, weights were recorded to the nearest mg, and the lizards were autopsied to determine reproductive condition. Ovaries and oviducal eggs were weighed, and clutch size was determined by counting yolked follicles ≥3 mm in diameter, oviducal eggs, and/or corpora lutea. In males the testes were weighed and their length and width measured. The amount of fat present and the weight of stomach contents of both sexes were also recorded. Stomach volume was determined by displacement of water in a graduated centrifuge tube and measured to the nearest 0.01 ml as described by Sanborn (1972). The stomach contents were separated and identified to family whenever possible, and their volume estimated.

RESULTS AND DISCUSSION

Reproduction

SEX RATIOS.—Sex ratios of *Cophosaurus* were skewed in favor of males in individuals ≥55 mm s-v, at 63:40, while in smaller individuals sexes occurred equally at 7:6. Sex ratios of adult *Callisaurus* at both Burro Creek and Rock Valley were close to one-to-one with male-to-female ratios of 53:50 and 42:40 for individuals ≥55 mm at Burro Creek and ≥60 mm at Rock Valley respectively. In contrast, sex ratios of younger *Callisaurus* from both localities were skewed in favor of females with sex ratios of 12:17 and 3:6 for Burro Creek and Rock Valley respectively.

Engeling (1972) concluded sex ratios of a population of marked *Cophosaurus* were equal. The disparity observed by us may be due to sampling error. Since male *Cophosaurus* often patrol, display, and observe from points of prominence, they would consistently be the most obvious and therefore the most commonly collected of the two sexes. The males are also larger and therefore easier to see. These arguments would also seemingly be true for *Callisaurus*, except that points of prominence are less common in the habitats most preferred by them. If it is true, however, it would agree with findings for the smaller-sized group with females being more common. If the females truly are more abundant in this species, the causes are unknown.

AGE AT MATURITY.—At Burro Creek during June and July no female *Cophosaurus* was found below the minimum reproductive size of 55 mm s-v. Only one *Callisaurus* was found below that s-v length, and it was a 52-mm female found on 1 June 1973. Similarly, no male *Cophosaurus* was found in June or July below the length of 55 mm s-v, and the smallest weight of testes was 0.043 g. In contrast, three *Callisaurus* from Burro Creek in early June were found to measure ≤55 mm, had testes weights of 0.013, 0.002, and 0.001 g, and were probably not yet reproductive. Similarly sized male *Callisaurus* were not found in late June or July.

At Rock Valley no female *Callisaurus* was collected below 60 mm s-v in the months of June or July. However, two females <55 mm collected in late May were not yet reproductive with ovarian weights of only 2 mg each. During June and July only one <60 mm *Callisaurus* male was collected. It was collected on 8 June, measured 56 mm s-v, and had a testes weight of only 2 mg. Engeling (1972), Ballinger et al. (1972), Howland (1984), Pianka and Parker (1972), and Tanner and Krogh (1975) agree that most sand lizards become reproductive as yearlings.

FEMALE REPRODUCTIVE CYCLE.—The first evidence of follicular development at Burro Creek in 1973 was exhibited by *Callisaurus* that contained yolked follicles 2 to 7 mm in diameter on 28 April. Unfortunately, comparable samples of *Cophosaurus* could not be obtained at this sampling period. By 1 June adequate populations of both *Callisaurus* and *Cophosaurus* were located in sympatry, and series of 10 and 13 respectively were collected. Reproductive condition of *Coph-osaurus* varied from small yolked follicles 3–5 mm in lizards <60 mm s-v to oviducal eggs in females >60 mm s-v. *Callisaurus* <60 mm were usually determined to be prereproductive, and females >60 mm s-v contained enlarged yolked follicles 3–9 mm in length or oviducal eggs. The reproductive season for both species apparently began by early May and was over in August. *Callisaurus* from Rock Valley probably ceased reproductive activities two to three weeks earlier than those at Burro Creek.

TABLE 1. Mean clutch size for various size groups of *Cophosaurus texanus* and *Callisaurus draconoides*, according to their availability.

Snout-vent length, mm	$\bar{x}$	Range	N
Cophosaurus texanus (Burro Creek)			
55–57	3.20(±0.45)	3–4	5
58–60	3.57(±0.79)	3–5	7
61–63	3.54(±0.88)	2–5	13
64+	4.00(±1.15)	3–5	4
All sizes	3.55(±0.83)	2–5	29
Callisaurus draconoides (Burro Creek)			
55–59	3.00	3	1
60–64	3.50(±0.58)	3–4	4
65–69	4.43(±1.09)	2–6	14
70–74	4.44(±1.13)	2–6	9
All sizes	4.25(±1.08)	2–6	28
Callisaurus draconoides (Rock Valley)			
65–69	4.00(±1.15)	3–5	4
70–74	4.82(±0.98)	3–6	11
75–79	5.22(±1.30)	3–7	9
80+	6.20(±1.64)	4–8	5
All sizes	5.07(+1.33)	3–8	29

Ballinger et al. (1972) found follicles in *Cophosaurus* from 8 April through 9 August and oviducal eggs from 27 April through 9 August. Engeling (1972) concluded that their reproductive season was from March through August. Howland (1984) stated that oviposition extended from mid-May to late August. In *Callisaurus*, Pianka and Parker (1972) found yolked follicles from April through September. Vitt and Ohmart (1977) found oviducal eggs from May through August with vitellogenesis beginning by mid-April. And Tanner and Krogh (1975) found follicles and oviducal eggs from late May into July, with most seen in June.

Table 1 shows the mean clutch size for various size groups of sand lizards. Mean clutch sizes for all size groups are 3.55 (±0.83) for *Cophosaurus* and 4.25 (±1.08) and 5.07 (±1.33) for *Callisaurus* at Burro Creek and Rock Valley respectively. There is a marked trend of an increase in clutch size with an increse in s-v length in both populations of *Callisaurus*, but this trend is not apparent in *Cophosaurus*. One record of a 69-mm *Callisaurus* collected on 8 September at Burro Creek with one 4-mm yolked follicle was deleted from this table, as it was not representative of the rest of the September sample and was the only record of a single-egged clutch. It is not known whether this ovum would have been deposited or resorbed.

The smallest *Cophosaurus* female found to be reproductive was 55 mm s-v with three yolked ovarian follicles 5 mm in diameter. The smallest reproductive *Callisaurus* from Burro Creek measured 58 mm s-v and contained three 7-mm follicles, while the smallest reproductive female from Rock Valley measured 65 mm s-v and had three oviducal eggs 17 mm long. Ballinger et al. (1972) and Engeling

TABLE 2. Clutch size and fat body weights (g) for female sand lizards ≥ 55 mm s-v. Date is mean date of collection.

Day and month	s-v range in mm (mean)	$\bar{x}$ clutch size	Range	N repro/ N examined	$\bar{x}$ fat body weight (S.D.)
Cophosaurus (Burro Creek)					
28 Apr	—	—	—	—	—
1 Jun	56–64(60.5)	3.55(±0.69)	3–5	10/13	.068(±.067)
23 Jun	55–64(60.3)	3.50(±1.07)	2–5	8/9	.056(±.041)
21 Jul	59–64(61.3)	3.60(±0.84)	3–5	9/9	.014(±.018)
8 Sep	—	—	—	0/5	.038(±.031)
6 Apr	—	—	—	0/3	.073(±.059)
Callisaurus (Burro Creek)					
10 Mar	—	—	—	0/4	.033(±.066)
7 Apr	—	—	—	0/5	.052(±.056)
28 Apr	67–70(68.8)	4.80(±0.84)	4–6	5/7	.161(±.105)
1 Jun	58–70(65.7)	4.29(±1.11)	3–6	6/9	.047(±.067)
23 Jun	60–70(65.0)	3.83(±0.41)	3–4	6/8	.073(±.057)
21 Jul	65–75(70.8)	4.20(±1.40)	2–6	9/9	.023(±.038)
8 Sep	—	—	—	0/6	.069(±.046)
6 Apr	—	—	—	0/2	.161(±.099)
Callisaurus (Rock Valley)					
2 May	72–82(77.0)	5.50(±2.12)	4–7	2/5	.153(±.115)
31 May	71–84(77.3)	6.25(±1.04)	5–8	6/7	.191(±.100)
8 Jul	65–82(72.9)	4.73(±1.01)	3–6	11/13	.197(±.223)
25 Jul	67–79(72.5)	4.25(±1.16)	3–6	8/12	.227(±.267)
13 Sep	—	—	—	0/1	.457

TABLE 3. Ranges of sizes of hatchling sand lizards found in September at Burro Creek, Mohave County, Arizona.

Species	Sex	Snout-vent length, mm	Weight, g
Cophosaurus	females	38–45	1.5–3.0
Cophosaurus	males	38–50	1.5–3.6
Callisaurus	females	30–46	0.7–3.3
Callisaurus	males	40–55	1.8–4.9

(1972) both found *Cophosaurus* to become reproductively mature at about 50 mm s-v, and Howland (1984) found them to mature between 52 and 55 mm s-v. Kay et al. (1970) found *Callisaurus* to become reproductive at 65 mm, Pianka and Parker (1972) recorded the smallest at 63 mm, and Tanner and Krogh (1975) found oviducal eggs in females as small as 66 and 67 mm s-v.

The mean clutch size of *Cophosaurus* has been variously reported at 2.8 (Hulse 1973), 3.1 (Howland 1984), 4.0 (Parker 1973), 4.6 (Vitt 1977), 5.0 (Johnson 1960), and 6.0–6.1 (Ballinger et al. 1972, Engeling 1972); and the pattern appears nonclinal and irregular as described by Fitch (1985). The mean clutch size of *Callisaurus* has been recorded at 4.4 (Pianka and Parker 1972), 4.5 (Vitt 1977, Tanner and Krogh 1975), and 4.6 (Vitt and Ohmart 1977), being apparently rather consistent throughout its range. The mean of 4.25 eggs per clutch recorded at Burro Creek then is a reported low associated with range periphery and the mean of 5.07 at Rock Valley a reported high probably associated with a short-term consideration of high precipitation, as with the increased fecundity found in *Uta* from the same location during that same year (Medica and Turner 1976).

Table 2 shows mean clutch size, number of animals found to be reproductive, and $\bar{x}$ fat body weights of female lizards sampled at various intervals. There was a trend for *Callisaurus* from Rock Valley to exhibit reduced fecundity through the breeding season. This trend was not as apparent for *Cophosaurus* and *Callisaurus* from Burro Creek. Peak periods of reproduction were in late July for both Burro Creek populations, while the *Callisaurus* from Rock Valley peaked in early July. Minimum mean fat body sizes were recorded for both *Cophosaurus* and *Callisaurus* at Burro Creek in the month of July, while the largest were recorded for both in the month of April. *Callisaurus* from Rock Valley maintained large fat bodies throughout the sampling period, probably due to unusually large amounts of precipitation presumably resulting in large quantities of food production during that year (Medica and Turner 1976). Vitt

Table 4. Reproductive data of *Cophosaurus* and *Callisaurus* based solely upon females carrying oviducal eggs. All mean values ± one standard deviation.

	Cophosaurus	*Callisaurus*	
		Burro Creek	Rock Valley
Number of females	12	6	10
$\bar{x}$ s-v length, mm	61.33 ± 2.02	67.0 ± 3.85	72.7 ± 4.97
$\bar{x}$ weight, g	8.169 ± 1.218	10.422 ± 1.405	13.375 ± 3.860
$\bar{x}$ clutch size	4.08 ± 0.79	4.50 ± 1.05	4.20 ± 1.48
$\bar{x}$ weight of clutch, g	1.270 ± 0.326	2.004 ± 0.574	2.255 ± 1.237
Clutch wt./body wt. ratio	0.155	0.192	0.169
$\bar{x}$ weight of one egg, g	0.319 ± 0.078	0.443 ± 0.039	0.517 ± 0.122
Egg wt./body wt. ratio	0.039	0.043	0.039

and Ohmart (1977) could find no clear pattern of fat body cycling in *Callisaurus* females.

Evidence of multiple clutches was exhibited by both species. A 56-mm *Cophosaurus* captured 2 June contained three yolked follicles 3 mm in diameter and three corpora lutea 1 mm in diameter. Another specimen 60 mm s-v captured on 21 July contained three 3-mm follicles and three 1-mm corpora lutea. Similarly, a 69- and a 65-mm *Callisaurus* from Burro Creek captured on 2 June and 21 July respectively both contained 3-mm ovarian follicles undergoing vitellogenesis as well as oviducal eggs 15 mm in length. From Rock Valley a 78-mm *Callisaurus* captured 24 May contained six 3-mm follicles and seven 17-mm oviducal eggs with corresponding corpora lutea. Another specimen 84 mm s-v from 4 June contained seven 4-mm follicles and eight corpora lutea measuring 2 mm. In addition to the six sand lizards already mentioned, four *Cophosaurus* between the dates of 1 June and 24 June, one *Callisaurus* from Burro Creek on 21 July, and one from Rock Valley on 13 July contained 2-mm follicles initiating vitellogenesis as well as oviducal eggs and/or corpora lutea. Given a reproductive period of at least three months, multiple clutches were probably common in Burro Creek populations of both species and *Callisaurus* of Rock Valley in 1973. The large range of sizes exhibited by hatchling sand lizards of both species in September at Burro Creek also supports this conclusion (Table 3). Engeling (1972) found *Cophosaurus* to hatch from June through October, and Whitford and Creusere (1977) reported similar findings.

Most investigators of these lizards have considered them to produce multiple clutches, but the evidence is more conclusive for *Cophosaurus* (Ballinger et al. 1972, Engeling 1972, Howland 1984, Johnson 1960, Vitt 1977) than for *Callisaurus* (Pianka and Parker 1972, Tanner and Krogh 1975). Vitt (1977) and this paper, however, present strong evidence for multiple clutches in *Callisaurus*.

Tinkle (1969, Tinkle et al. 1970) has elucidated the concept of reproductive effort and its adaptive and evolutionary significance as it applies to lizard populations. To facilitate these considerations, we have also tabulated reproductive data (Table 4) based solely on females carrying oviducal eggs. In comparison with published accounts, the Burro Creek populations of *Cophosaurus* and *Callisaurus* and the Rock Valley *Callisaurus* exhibited egg weight/body weight ratios of 0.039, 0.043, and 0.039 respectively that are much lower than 0.056 and 0.058 for *Cophosaurus* and *Callisaurus* presented by Vitt (1977). The clutch weight/body weight ratio of 15.5% for *Cophosaurus* is also much lower than the 21.8% presented by Ballinger et al. (1972) for a population of *Cophosaurus* in Texas. In further contrast to Ballinger et al. (1972), we did not find the mean weight of eggs of *Cophosaurus* to be smaller in smaller females. In fact, we generally found the opposite to be true, but not significantly so. The smallest mean oviducal egg weights of 0.171, 0.197, 0.242, and 0.287 were associated with females having s-v lengths of 64, 64, 59, and 63 mm respectively, and 64 mm was the largest s-v length for a female of this species at Burro Creek. All four of these small mean egg weights were associated with large clutches of five eggs each. The largest mean egg weight of 0.409, however, was obtained from a 62-mm female, also with five eggs.

Male reproductive cycle.—Table 5 shows testicular measurements and fat body

TABLE 5. Testicular size (mm) and fat body weight for male sand lizards ≥60 mm s-v. Day is mean date of collection.

Day and month	s-v range in mm (mean)	N	x̄ testes length × width (mm)	x̄ testes weight (S.D.) (g)	x̄ fat body weight (S.D.)(g)
Cophosaurus (Burro Creek)					
28 Apr	67–71(68.7)	3	6.3 × 4.3	.082(±.020)	.054(±.012)
1 Jun	60–74(67.7)	20	6.5 × 5.2	.090(±.023)	.059(±.048)
23 Jun	60–70(66.2)	6	6.3 × 4.5	.077(±.021)	.014(±.009)
21 Jul	62–77(68.3)	13	6.4 × 5.1	.091(±.024)	.027(±.044)
8 Sep	61–70(65.4)	11	3.0 × 2.0	.003(±.002)	.109(±.108)
6 Apr	62–69(65.0)	4	5.5 × 4.3	.050(±.013)	.033(±.023)
Callisaurus (Burro Creek)					
3 Mar	65–75(71.3)	4	4.0 × 3.0	.038(±.033)	.004(±.005)
7 Apr	74–76(75.0)	2	6.0 × 4.5	.102(±.036)	.007(±.009)
28 Apr	66–81(74.5)	6	7.7 × 6.2	.175(±.046)	.057(±.061)
1 Jun	63–84(76.7)	6	7.0 × 5.2	.147(±.046)	.027(±.048)
23 Jun	62–83(75.7)	7	6.9 × 5.3	.105(±.039)	.067(±.084)
21 Jul	74–84(77.8)	12	7.4 × 5.3	.118(±.033)	.031(±.048)
8 Sep	70–75(72.8)	5	3.2 × 2.0	.003(±.002)	.092(±.075)
6 Apr	61–82(75.0)	4	5.5 × 4.0	.079(±.059)	.035(±.027)
Callisaurus (Rock Valley)					
27 Apr	64–87(79.6)	10	7.2 × 5.5	.159(±.086)	.132(±.198)
6 Jun	77–89(83.1)	8	8.6 × 6.3	.256(±.074)	.210(±.114)
8 Jul	68–94(82.6)	16	6.3 × 4.9	.139(±.167)	.273(±.247)
25 Jul	79–90(85.3)	6	5.8 × 3.8	.057(±.016)	.514(±.249)
13 Sep	77	1	5 × 2	.023	1.076

weights of male lizards from Burro Creek and Rock Valley. Minimum testicular measurements were obtained during the month of September in all populations. Maximum testicular measurements were obtained for *Cophosaurus* on 1 June and 21 July, for *Callisaurus* at Burro Creek on 28 April, and for *Callisaurus* from Rock Valley during early June. Maximum mean fat body sizes were obtained in the month of September for all populations. Minimal measurements were obtained for *Cophosaurus* on 23 June, in March and April for *Callisaurus* from Burro Creek, and in April for *Callisaurus* from Rock Valley; however, as with females, fat bodies of males from Rock Valley were enlarged throughout 1973.

The male reproductive cycles of both lizards have been well studied (Shrank and Ballinger 1973, Pianka and Parker 1972, Tanner and Krogh 1975, Vitt and Ohmart 1977), and for the most part our results are comparable. However, the maintenance of enlarged fat bodies throughout the reproductive season by *Callisaurus* at Rock Valley is unusual and probably reflects an unusually good food supply at that locality for that year.

FOOD HABITS

We have compared food habits of *Cophosaurus texanus* and *Callisaurus draconoides* from Burro Creek at two levels. First, we compared the orders of organisms eaten during the entire sampling period (Figs. 1 and 2). Secondly, we compared orders of organisms consumed on a monthly basis (Table 6).

Upon comparison of the pie diagrams, we find that insects comprised over 90% of the diet for both species. However, the quantities of each order consumed by each species varied considerably. Almost 50% of the diet of *Callisaurus* consisted of Orthoptera and Lepidoptera, whereas *Cophosaurus* consumed 18% Orthoptera, about 16% Hymenoptera, and only 10% Lepidoptera and also displayed considerably more dependency upon Coleoptera and Araneida than did *Callisaurus*. Niche overlap, based on these data and calculated using the formula of Pianka (1973, 1974), is high at 0.88.

Our findings at the familial level (unpublished data) indicate that niche overlap for these resources in reality may not be this high. Although both species were observed in

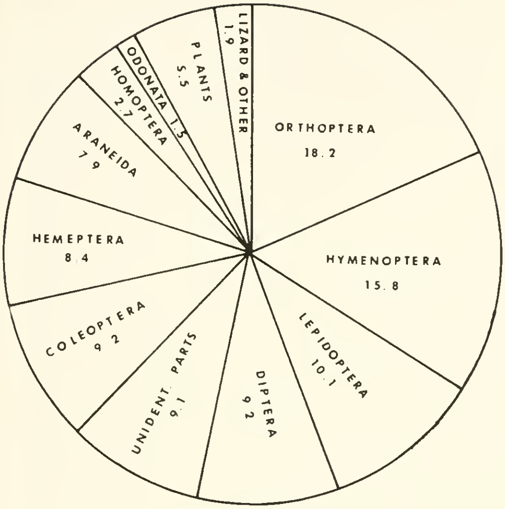

Fig. 1. Food habits of *Cophosaurus texanus* during 1973 and 1974, indicating percent volume of each category.

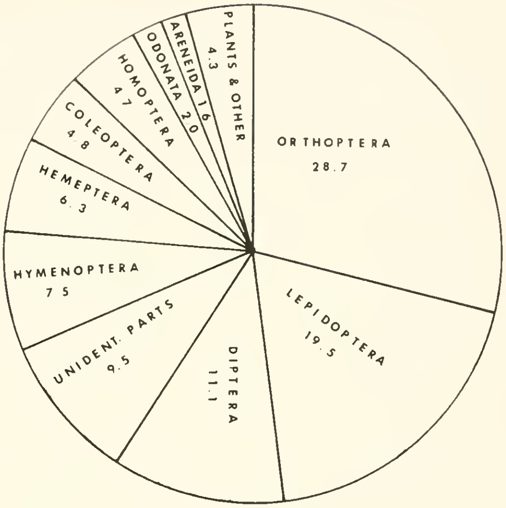

Fig. 2. Food habits of *Callisaurus draconoides* during 1973 and 1974, indicating percent volume of each category.

the riparian habitat (see Activity), *Cophosaurus* tended to feed closer to the stream than did *Callisaurus.* For example, in the Orthoptera we find that both species ate acridids, but *Cophosaurus* consumed far fewer acridids than did *Callisaurus.* Instead, *Cophosaurus* was found to feed heavily upon tetrigids and tridactylids. In the Coleoptera we saw a similar trend, for of the two lizards only *Cophosaurus* consumed hydrophilids, omophronids, and psephenids. This trend was not as obvious in other families because they are not characterized by their occurrence in limnological habitats. This may also explain the greater volume of both Hymenoptera and Araneae in *Cophosaurus,* for there was probably a greater diversity and abundance of members of both these groups in the riparian habitat. Therefore, it is probable that *Callisaurus* feeds in the more xeric areas of the riparian habitat as indicated by the greater occurrence of acridids, lygaeids, and formicids.

During the late summer and early spring when hatchling lizards were abundant, we found that *Cophosaurus* occasionally supplemented their diet with vertebrate prey, particularly *Urosaurus ornatus.* No vertebrates were found in the stomachs of *Callisaurus.* Table 6 indicates that the diets of these two lizards are highly variable, and they are probably greatly influenced by blooms, hatches, and phenology as it relates to populations of appropriately sized and edible insects. Throughout the activity season, however, Orthoptera seemed to constitute the primary food source of both species.

Engeling (1972) found that *Cophosaurus* most frequently ate orthopterans, hemipterans, coleopterans, and araneans. Pianka and Parker (1972) found *Callisaurus* to feed primarily on orthopterans and coleopterans in the U.S. and insect larvae and hymenopterans in Sonora, Mexico. Vitt and Ohmart (1975) found *Callisaurus* to primarily feed on orthopterans, and to a small extent (<1%) on small lizards. Tanner and Krogh (1975) and Kay et al. (1970) found *Callisaurus* to primarily feed upon hymenopterans and dipterans respectively. Pack (1923) found 10% of the food items consisted of vegetable matter, and 89% consisted of insects, with hymenopterans, lepidopterous larvae, neuropterans, hemipterans, and coleopterans represented in that order.

ACTIVITY

Habitat preference.—The plant association in which the lizards were first encountered gives an indication as to which habitat was preferred at Burro Creek. Table 7 indicates that *Cophosaurus* was primarily found in the riparian habitat (77.9%) and secondarily in the arroyos (14.2%), being usually re-

TABLE 6. Food habits of *Cophosaurus texanus* (*Coph.*) and *Callisaurus draconoides* (*Call.*) for 1973 and 1974 at Burro Creek, Mohave County, Arizona, indicating the percent volume of each category.

	March 1973	April 7, 1973		April 28, 1973		June 1, 1973		June 23, 1973	
Taxon	*Call.*	*Coph.*	*Call.*	*Coph.*	*Call.*	*Coph.*	*Call.*	*Coph.*	*Call.*
ARACHNIDA									
Araneida	5.7	—	2.1	—	1.3	7.5	2.2	11.2	1.7
INSECTA									
Thysanura	—	—	—	—	—	0.2	—	—	—
Odonata	—	—	—	—	—	—	—	—	—
Orthoptera	0.4	—	—	21.4	25.8	4.7	22.0	32.8	42.4
Isoptera	—	—	—	—	—	—	—	—	—
Hemiptera	2.1	—	1.6	—	4.4	7.7	18.6	4.3	7.0
Homoptera	2.1	—	—	—	—	0.6	0.4	0.7	2.1
Neuroptera	—	—	—	4.3	0.7	1.3	0.8	—	0.6
Coleoptera	2.1	—	2.1	—	0.4	9.3	2.8	10.7	2.5
Lepidoptera	38.9	—	46.6	28.6	44.7	11.5	16.4	24.9	0.9
Diptera	28.2	83.3	34.1	—	14.2	15.4	12.0	2.6	2.5
Hymenoptera	5.4	—	6.8	42.9	2.2	31.2	13.6	1.2	10.9
Unidentified parts	7.1	—	6.2	2.9	6.0	5.9	6.8	7.8	28.8
ISOPODA	—	—	—	—	—	—	2.4	—	—
PLANT MATERIAL	7.9	16.7	0.6	—	—	4.7	2.0	3.8	0.9
LIZARD (skin, parts)	—	—	—	—	—	—	—	—	—

stricted to the edges. *Callisaurus*, on the other hand, preferred the arroyos (57%), which have the largest expanses of open sandy spaces; secondarily they utilized the riparian association (40.7%).

The soil/substrate type in the riparian association is sand interspersed with numerous boulders, and this substrate was preferred by *Cophosaurus* 69.0% of the time. *Callisaurus* prefers the more open sandy areas and was taken on such substrate 72.0% of the time.

Niche overlap calculated by the formula of Pianka (1973, 1974) is higher based on habitat preference (0.71) than on the microhabitat determination of soil/substrate type (0.57). Therefore spatial partitioning is greatest at the level of the microhabitat, with *Cophosaurus* being characterized as more saxicolous than *Callisaurus*. Similar preferences have also been observed by Clarke (1965) and Engeling (1972), who noted the preferred habitat of *Cophosaurus* was dry creek beds with a preponderance of flat-surfaced limestone and sandstone. Pianka and Parker (1972) and Tanner and Krogh (1975) noted that *Callisaurus* preferred open areas of desert flats and valleys. Whitford and Creusere (1977) found *Cophosaurus* to be a permanent resident of the arroyo-shrub association and a transient resident in open *Larrea*.

TIME OF ACTIVITY.—Table 8 shows the frequency of collection of *Cophosaurus* and *Callisaurus* at Burro Creek during 12 daily time intervals. *Cophosaurus* was most active between 0900 and 1300 hr with another period of activity initiated after 1700 hr. *Callisaurus* probably initiated activity a little earlier than *Cophosaurus* and decreased activity about 1200 hr. Also, they exhibited a less-pronounced peak of evening activity. Temporal niche overlap calculated by the formula of Pianka (1973, 1974) is high at 0.86.

Engeling (1972) found *Cophosaurus* most active in the afternoon, but some activity was observed at nearly all hours of the day between 0919 and 1948 hr. Pianka and Parker (1972) found *Callisaurus* active as early as 0730 and suggested bimodal diel activity. Tanner and Krogh (1975) found *Callisaurus* rather heat tolerant, seldom active before 0800, and considered them to remain active throughout the heat of the day. Kay (1970), who has probably done the most extensive activity study, found *Callisaurus* to be active throughout the day, but showing weak bimodality through the summer.

TEMPERATURE RELATIONSHIPS.—The mean body temperature of *Cophosaurus texanus* was 38.5 C (±1.5, n = 73) and of *Callisaurus draconoides* was 38.2 C (±2.4, n = 96). The mean surface soil temperature and air temperature within 2 cm of the soil at the point of capture were 42.0 C (±5.1, n = 69) and 36.0 C (±4.4, n = 68) for *Cophosaurus*, and 40.5 C

Table 6 continued.

July 21, 1973		Sept. 8, 1973		April 7, 1974	
Coph.	*Call.*	*Coph.*	*Call.*	*Coph.*	*Call.*
14.3	0.3	1.6	0.4	3.3	0.8
—	—	—	—	—	—
—	—	6.3	16.8	4.0	—
28.2	54.6	39.2	44.8	5.7	1.1
—	—	1.1	3.2	—	—
1.9	1.6	2.9	7.4	31.6	11.4
11.1	21.8	—	0.6	—	1.2
—	—	—	—	—	—
5.6	8.4	16.5	7.1	7.5	18.4
4.3	3.1	2.5	1.1	9.8	4.1
5.1	0.7	3.6	1.1	4.0	4.5
7.6	2.2	4.0	9.9	12.9	17.6
12.7	6.9	13.4	7.1	9.7	4.5
—	—	—	—	—	—
4.1	—	5.4	0.4	10.9	36.3
5.1	—	3.4	—	—	—

(±7.8, n = 90) and 35.8 C (±5.0, n = 65) for *Callisaurus* respectively. There are no differences in these respective pairs of means between *Cophosaurus* and *Callisaurus* at the .05 level of significance.

Clarke (1965) found the mean body temperature of *Cophosaurus* to be 38.3 C and 39.2 C for *Callisaurus* and related this difference to geographic distribution, with *Callisaurus* generally living in the warmer locales. Most other studies have also found the mean or median body temperature for *Callisaurus* to be 39.1 C or slightly higher (Packard and Packard 1970, Pianka and Parker 1972, Tanner and Krogh 1975). We conclude from our data that there is virtually no difference in the temperature responses of the two species when exposed to the same or similar ambient temperatures as with the two populations at Burro Creek. Muth (1977a, 1977b) has correlated and analyzed body temperatures and associated posturing in *Callisaurus*.

SUMMARY AND CONCLUSIONS

From this study a number of conclusions can be drawn concerning the biology of *Cophosaurus* and *Callisaurus* at Burro Creek and *Callisaurus* at Rock Valley. Sex ratios of adult *Cophosaurus* were unequal in our samples, with a larger number of males being present. This, however, may have been due to sampling error and the fact that males are more obvious. Sex ratios of adult *Callisaurus* from both Burro Creek and Rock Valley were approximately equal, but in samples of juveniles, females outnumbered males.

Most males and females of both species became reproductively mature after their first hibernation. Reproductive seasons last from April through August, and mean clutch sizes of 3.55, 4.25, and 5.07 were determined for *Cophosaurus* and *Callisaurus* from Burro Creek and Rock Valley respectively. Multiple clutches were probably common among individuals of both species, but evidence for this at Rock Valley was found only in larger and presumably older adults. Also, the reproductive season is probably terminated two to three weeks earlier in this northern population.

Mean egg size of both species of lizards and clutch size/body weight ratios of *Cophosaurus* were determined to be smaller than reported previously from other populations (Vitt 1977, Ballinger et al. 1972).

The male reproductive cycles of both species were found to be similar to those previously reported. However, corpora adiposa of both male and female *Callisaurus* from Rock Valley remained relatively large throughout the summer, presumably because of abundant food at that locality in 1973.

The food habits of both *Cophosaurus* and *Callisaurus* at Burro Creek are similar, but they are probably greatly influenced by sporadic and episodic availability. Both lizards are highly insectivorous with Orthoptera being the staple food during the summer months.

Differences between preference of macrohabitat and microhabitat were observed, *Callisaurus* preferring sandy open areas and *Cophosaurus* preferring the presence of some rocks and boulders. Both lizards maintained similar daily activity patterns. *Callisaurus* may initiate activity earlier in the day than *Cophosaurus*, but some *Cophosaurus* tend to remain active throughout the day. *Cophosaurus* has a more pronounced activity period in the evening than was observed for *Callisaurus*. Temperature relationships are very similar for the two species.

Niche overlap for the two populations at Burro Creek was calculated at 0.71, 0.57, 0.86, and 0.88 at the levels of macrohabitat,

TABLE 7. Habitat preferences of *Cophosaurus* and *Callisaurus* at Burro Creek, based upon plant associations and soil type. Figures are frequency of encounters in percent.

Plant association	*Cophosaurus*	*Callisaurus*
Riparian	77.9	40.5
Arroyo	14.2	56.9
Acacia	—	1.7
Paloverde-Sahuaro	7.9	0.9
Totals	100.0	100.0
Soil/substrate type		
Sand	24.8	72.0
Gravel	6.2	8.8
Boulders	69.0	19.2
Totals	100.0	100.0

TABLE 8. Frequency of collections of *Cophosaurus* and *Callisaurus* at 12 daily time intervals at Burro Creek.

	Cophosaurus		*Callisaurus*	
Time interval	N	Percent frequency	N	Percent frequency
0700–0759	0	0.0	3	2.3
0800–0859	4	3.5	10	7.8
0900–0959	13	11.3	39	30.2
1000–1059	29	25.2	34	26.4
1100–1159	22	19.1	20	15.5
1200–1259	18	15.7	10	7.8
1300–1359	5	4.3	6	4.7
1400–1459	2	1.7	0	0.0
1500–1559	3	2.6	0	0.0
1600–1659	2	1.7	0	0.0
1700–1759	10	8.7	1	0.8
1800–1859	7	6.1	6	4.7
Totals	115	99.9	129	100.2

microhabitat, time of activity, and food habits respectively. The values of microhabitat and temporal overlap are very similar to the mean values for North American lizards calculated by Pianka (1973) at 0.55 and 0.86 respectively. But niche overlap at the trophic level is much higher at Burro Creek at 0.88 compared to Pianka's mean value of 0.49. It is probable that the productive environs associated with the riparian habitat in an otherwise desert community are responsible for the coexistence of these two similar sand lizards at Burro Creek.

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ZOOGEOGRAPHY OF GREAT BASIN BUTTERFLIES: PATTERNS OF DISTRIBUTION AND DIFFERENTIATION

George T. Austin[1] and Dennis D. Murphy[2]

ABSTRACT.—The butterflies of the Great Basin exhibit general patterns of distribution and speciation similar to those found for other taxa, particularly birds. Two major centers of infraspecific differentiation and coinciding distribution limits of taxa are identified, each with three subregions. Great Basin butterflies are characterized by pallidity and substantial endemism below the species level.

The Great Basin of western North America is a huge area, nearly 520,000 square kilometers, of largely internal drainage between the Rocky Mountains to the east and the Sierra Nevada to the west. It includes Utah west of the Wasatch Plateau, extreme southwestern Idaho and southeastern Oregon, California east of the Sierra Nevada, and nearly all of Nevada (Fig. 1). Elevations range from 1,000-m lowlands dominated by sagebrush (*Artemisia*) and saltbush (*Atriplex*) to numerous, mostly north-south oriented mountain ranges which may exceed 3,000 m. These mountain ranges, most of which are forested only at the higher elevations, constitute islands of boreal habitat. Lowland wet areas are similarly islandlike. The area is largely uninhabited by humans and is relatively undisturbed except for livestock grazing which has had substantial impact on the composition of the vegetation, especially at lower elevations (e.g., Rogers 1982, Thomas 1983).

Studies of the distribution and biogeography of Great Basin biota have dealt largely with vertebrates (e.g., Behle 1963, 1978, Brown 1971, 1978, Grayson 1982, 1983, Johnson 1975, 1978, Smith 1978) and plants (e.g., Billings 1978, Harper et al. 1978). Here we present information on the distribution of Great Basin butterflies, paying particular attention to the distributional limits of species, subspecies, and well-differentiated segregates, and to centers of infraspecific differentiation. Additionally, we discuss the role of "island" effects in shaping local species richness.

MATERIALS AND METHODS

Distribution maps for butterfly taxa and other distinct phenotypes occurring within and on the margins of the Great Basin were constructed from a variety of sources. Nevada data are drawn primarily from the collections and field notes at the Nevada State Museum, Carson City, the senior author's personal collection, and collections made by the Center for Conservation Biology at Stanford University. Eastern California data were obtained from the notes and collections of a number of private collectors. Southern Oregon records are from Dornfeld (1980), and Rocky Mountain and eastern Great Basin records are from Ferris and Brown (1981). Some Sierra Nevada data were obtained from Shapiro et al. (1979) and the collections of the Nevada State Museum. Numerous other literature sources were consulted.

The maps thus prepared were examined to determine patterns of distribution within the Great Basin and adjacent areas. Attention was paid to the absence or presence of species within the Great Basin and the extent of their apparent distributions and differentiation in the Great Basin.

TAXA AND DISTRIBUTION

The 155 butterfly species occurring in the Great Basin include some 240 subspecies and well-differentiated segregates. More than half the species are geographically polytypic in this and adjacent regions, including the Rocky

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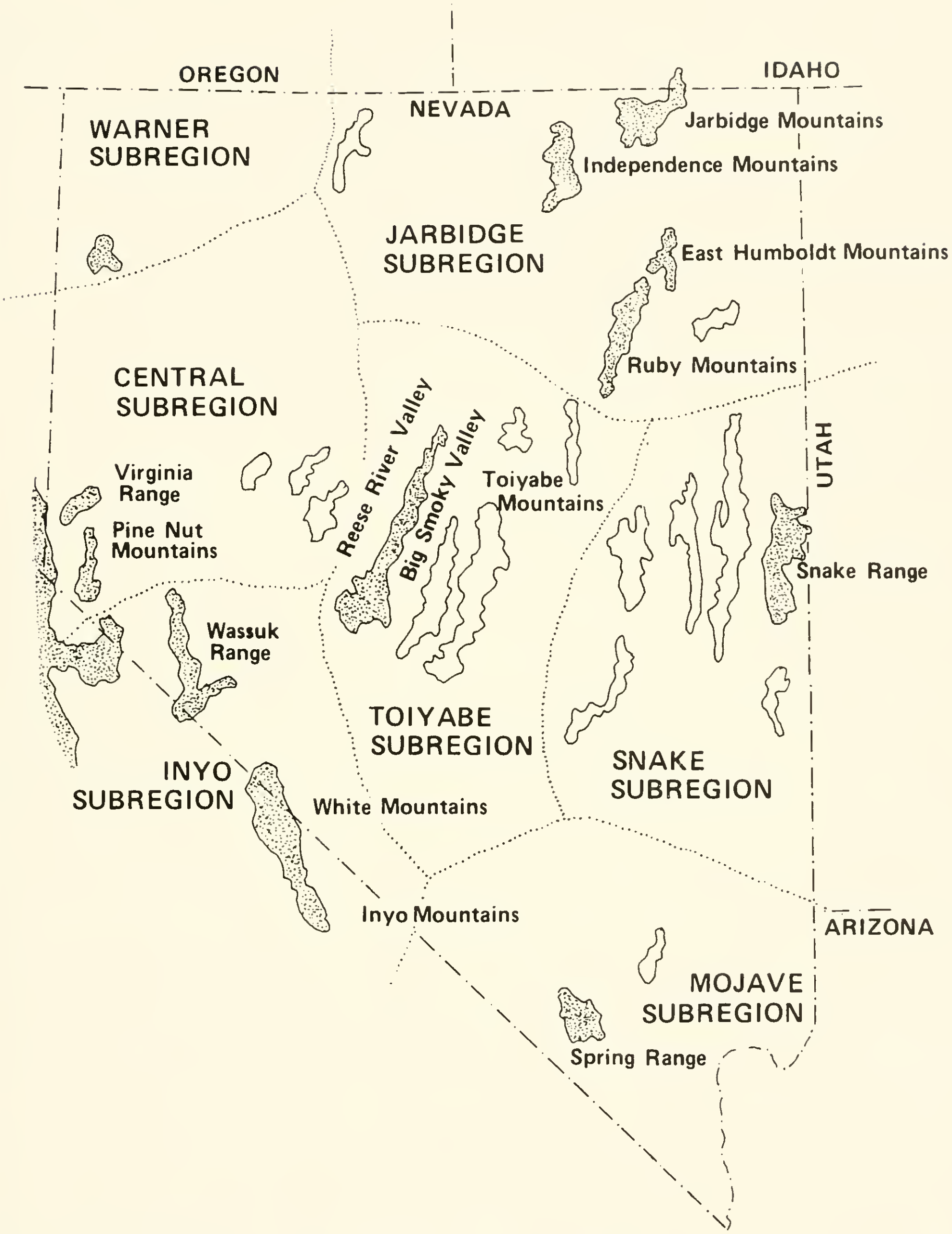
OREGON
IDAHO
NEVADA
WARNER SUBREGION
Jarbidge Mountains
Independence Mountains
JARBIDGE SUBREGION
East Humboldt Mountains
CENTRAL SUBREGION
Ruby Mountains
UTAH
Reese River Valley
Big Smoky Valley
Virginia Range
Toiyabe Mountains
Pine Nut Mountains
Snake Range
Wassuk Range
TOIYABE SUBREGION
SNAKE SUBREGION
INYO SUBREGION
White Mountains
Inyo Mountains
ARIZONA
MOJAVE SUBREGION
Spring Range

Fig. 1. The Great Basin showing subregions and locations mentioned in the text.

Mountains and Sierra Nevada. No species are endemic to the Great Basin, consistent with previous findings for birds (Behle 1963). About 50 subspecies and other well-differentiated infraspecific segregates (distinct groups of phenotypically similar, but unnamed, populations) of butterflies, however, are restricted to the Great Basin. A number of additional groups of populations within the region show some measurable differentiation. The distributions of these taxa and segregates by geographic affinities are summarized in Table 1.

Nearly 90% of all Great Basin butterfly species are also found in the Rocky Mountains.

TABLE 1. Affinities of the Great Basin butterfly fauna. Taxa include subspecies and distinct unnamed segregates.

	Species		Taxa	
Sierra Nevada	8	(5.2%)	35	(14.5%)
Rocky Mountain	30	(19.3%)	67	(27.8%)
Widespread (including Sierra Nevada and Rocky Mountains)	99	(63.8%)	48	(19.9%)
Endemic	0	(0.0%)	52	(21.6%)
Southern	15	(9.7%)	29	(12.0%)
Northern	3	(1.9%)	10	(4.1%)
TOTAL NUMBER	155		241	

TABLE 2. Widespread Rocky Mountain and Sierra Nevada butterfly species absent or nearly so from the Great Basin.

Epargyreus clarus
Thorybes pylades
Thorybes mexicana
Erynnis pacuvius
Pyrgus ruralis
Polites sonora
Euphyes vestris
Amblyscirtes vialis
Parnassius clodius
Lycaena mariposa
Plebejus idas
Plebejus franklini
Speyeria hydaspe
Boloria epithore
Chlosyne palla
Polygonia faunus

Only about two-thirds of the Great Basin butterfly species occur in the Sierra Nevada. When considering truly widespread Great Basin taxa as opposed to those occurring merely on the margins, Great Basin butterflies shared with the Rocky Mountains outnumber those shared with the Sierra Nevada by about three to one.

Great Basin butterflies are made up of several distinct groups:

1. A large number of relatively widespread species which occur in the Great Basin as endemic subspecies or segregates (many of which represent the species' most pallid phenotype). This in itself identifies the Great Basin as a distinct region of differentiation for butterflies.

2. A group of widespread species which occur throughout much of the western portion of the continent. The majority of these species show little or no regional differentiation.

3. A number of desert taxa extending into the Great Basin from the south, reaching their northern limit there and either occurring only along the southern fringe of the basin or ranging further north as permanent populations, seasonal populations, or stray individuals. Many other species occur just south of the Great Basin in extreme southern Nevada and southwestern Utah (e.g., Austin and Austin 1980).

4. And, finally, there are a few butterflies of mainly northern affinity that range south into the Great Basin. Nearly all of these are limited to the northern portion of the Great Basin.

The Great Basin butterfly fauna is characterized not only by the presence of numerous endemic phenotypes but by the restricted distribution or conspicuous absence of certain taxa. The borders of the Great Basin additionally provide range limits for a large number of species. An indication of this can be seen in Scott's (1986) "spaghetti diagram" of the entire North American fauna. Some, particularly desert, species are apparently prevented from entering the region by climatic factors either directly limiting the butterflies or their larval host plants. Severity of Great Basin winters is probably one such factor, but this does not explain all absences. Many other species might be expected at specific locations within the Great Basin where suitable conditions seem to exist.

At least 16 species that occur on the very fringes of the Great Basin (Table 2) are widely distributed in the Rocky Mountains, west to Oregon and south through the Cascades to the Sierra Nevada. Other species exhibit a similar northern distribution pattern but do not occur in either the Rockies or Sierra Nevada. These absences from the Great Basin may be due to interacting factors that include climate, absence or paucity of suitable habitats and host plants, and the inability of these species to disperse across expanses of desert (i.e., Holdren and Ehrlich 1982). Still another possibility is that some species once occurred in the Great Basin but have been extirpated by increasing aridity and concomitant habitat constriction following the Pleistocene (e.g., Wells 1983). Noteworthy, however, is that few species show disjunct distribution patterns suspected to be relictual. *Pholisora catullus*, *Speyeria egleis*, *Lycaena nivalis*, and *L. editha* are found in the Toiyabe Mountains of Lander and Nye counties, Nevada. The clos-

Table 3. Distribution of Great Basin endemic butterflies by region.[1]

Eastern Region

Jarbidge
Ochlodes sylvanoides bonnevilla
*_Lycaena editha nevadensis_
*_Euphilotes rita mattonii_
*_Speyeria atlantis greyi_
*_Speyeria atlantis elko_
Speyeria mormonia artonis
Phyciodes campestris seg.
Euphydryas colon nevadensis

Snake
Polites sabuleti seg.
Satyrium saepium seg.
*_Incisalia augustus_ (?) seg.
*_Euphilotes battoides_ seg.

Toiyabe
Polites sabuleti seg.
Papilio indra nevadensis
*_Speyeria egleis toiyabe_
*_Cercyonis oetus pallescens_

Widespread
Euphydryas editha lehmani
Euphydryas editha koreti

Western Region

Inyo
Thorybes mexicana blanca
*_Hesperia miriamae_ seg.
*_Polites sabuleti_ seg.
Lycaena rubidus seg.
Euphilotes mojave langstoni
*_Plebejus icarioides_ seg.
*_Plebejus saepiolus_ seg.
Coenonympha ochraceae mono
*_Cercyonis pegala wheeleri_
Neominois ridingsii seg.

Central
*_Pseudocopaeodes eunus_ seg.
*_Polites sabuleti genoa_
*_Euphilotes rita_ seg.
Speyeria zerene malcolmi
Speyeria callippe nevadensis
Euphydryas editha monoensis
*_Cercyonis pegala_ seg.

Warner
Polites sabuleti seg.
*_Polites sabuleti_ seg.
*_Pieris napi_ seg.
Lycaena rubidus rubidus
Cercyonis pegala stephensi

Widespread
Hesperia uncas macswaini

Widespread in Great Basin
Colias alexandra edwardsii
Lycaena arota virginiensis
Mitoura siva chalcosiva
Euphilotes battoides baueri
Euphilotes rita pallescens
Glaucopsyche piasus nevada
Speyeria nokomis apacheana

Table 3 continued.

Speyeria zerene gunderi
Limenitis archippus lahontani
Cercyonis sthenele paulus
Neominois ridingsii stretchii

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[1] Here and in subsequent tables, seg. (segregate) is used to denote distinct sets of phenotypically similar populations which are as yet unnamed
*Narrowly distributed taxon

est extant populations apparently are now well to the north. *Papilio indra*, in addition, exists as a relatively isolated endemic subspecies in the same general area, and *Plebejus lupini* occurs as widely scattered populations across central Nevada. Several of these same species also extend into montane areas south of the Sierra Nevada cordillera (Emmel and Emmel 1973), indicating an ability to survive in more xeric conditions than those at their distribution centers.

Centers of Differentiation

A number of Great Basin species are comparatively unvarying in phenotype over a broad area from the Rocky Mountains or eastward, west to the Sierra Nevada or beyond. Others exhibit considerable regional differentiation and may include one or more phenotypes restricted to the Great Basin. The large number of phenotypic endemics suggests that the Great Basin is at least a moderately active area of infraspecific differentiation. Examination of the distributions of subspecies and segregates of polytypic species in the Great Basin and adjacent butterfly faunas shows rather well defined distribution patterns suggesting "centers of differentiation." Similar to Behle's (1963) findings for birds, these centers are bounded by areas where numerous range limits coincide, further suggesting that the Great Basin consists of definable biogeographical units (Fig. 1, Table 3). These regions generally coincide with distributional limits or more widespread butterfly taxa and are strikingly similar to distributional centers found for birds (Behle 1963, 1978).

Eastern Region

The Great Basin may be viewed as two distinct centers of butterfly distribution and differentiation (Fig. 1). The first is the Eastern Region bounded by the Wasatch Front in the east, to and including the Reese River Valley and from the northern limits of the Mojave Desert in the south, north to southern Idaho and southeastern Oregon. The area includes the Pleistocene Lake Bonneville basin, eastern portions of the Pleistocene Lake Lahontan basin, the Ruby group of drainages, and the southern portion of the Snake River drainage group (see Smith 1978). This region is comprised of three subregions: (1) the Jarbidge Subregion (southern Snake, northern Bonneville, and northeastern Lahontan drainages)—including the area north of the Humboldt River to central Humboldt County in Nevada, adjacent southeastern Oregon, southern Idaho, and northwestern Utah; (2) the Snake Subregion (Ruby and southern Bonneville drainages)—including the remainder of the Great Basin along the eastern border of Nevada and western Utah; and (3) the Toiyabe Subregion (southeastern Lahontan drainage)—including the central portion of Nevada. The Eastern Region loosely corresponds to Behle's (1963) concept; however, he did not subdivide the region, and he included more of Idaho.

The most clearly defined center of differentiation in the Eastern Region is the Jarbidge Subregion. Three subspecies are narrowly restricted to the Jarbidge and Independence ranges and another to the Ruby and East Humboldt ranges (Table 3). Three other subspecies and one segregate are distributed more broadly in the subregion. The Snake Subregion has two apparent narrowly distributed segregates in the vicinity of the Snake Range and two others more widely distributed. The Toiyabe Subregion has two narrowly distributed subspecies and one subspecies and one segregate more widespread. Two other endemic Great Basin subspecies are more widely distributed in the Eastern Region, ranging into two or more of the subregions.

Western Region

This region includes the area from the western edge of the Eastern Region (defined above) to the east slope of the Sierra Nevada, north from the Mojave Desert to south central Oregon (Fig. 1). The area includes the western portion of the Pleistocene Lake Lahontan basin and the southern Oregon Lakes drainage group (Smith 1978). Again three subregions may be discriminated: (1) the Inyo Subregion (southwestern Lahontan basin)—including the White Mountains and adjacent areas, Wassuk and Sweetwater mountains, and adjacent east slope of the Sierra Nevada of Nevada and California; (2) the Warner Subregion (southern Oregon Lakes drainage)—including northeastern California, northwestern Nevada, and south central Oregon; and (3) the Central Subregion (west central and northwestern Lahontan basin)—the area between the above (Fig. 2). Behle (1963) excluded, but later included (Behle 1978), the Inyo and Warner subregions in the Western Region and discussed them as separate biogeographic entities (see also Miller 1941, Johnson 1970).

The Inyo Subregion is the most well defined center of butterfly differentiation in the Western Region (Table 3). Speciation in this area is greatest in the White Mountains where at least one endemic subspecies and four endemic segregates are recognizable. Another subspecies is restricted to the Owens Valley. An additional four subspecies are more widely distributed in the subregion.

The Warner Subregion has at least two endemic subspecies and three endemic segregates. The Central Subregion is geographically broad and not sharply defined. There are three restricted segregates and one restricted subspecies and three more widely ranging subspecies, some of which extend for varying distances into the Inyo and/or Warner subregions. One additional subspecies is relatively widespread throughout the Western Region.

Finally, 11 endemic Great Basin subspecies occur in at least one (usually more) subregion of both the Eastern and Western regions.

SPECIATION PHENOMENA

Zones in which subspecies or segregates interface are found throughout the Great Basin. Some, however, emerge prominently as areas of intergradation for a wide variety of species when distribution and differentiation patterns are examined. Similar phenomena were identified and discussed for birds by Johnson (1978). Here we follow that presentation for butterflies. Areas where speciation appears to be less obvious coincidently have been less well studied. But, while further knowledge may somewhat alter the details, the overall definition of these zones and the

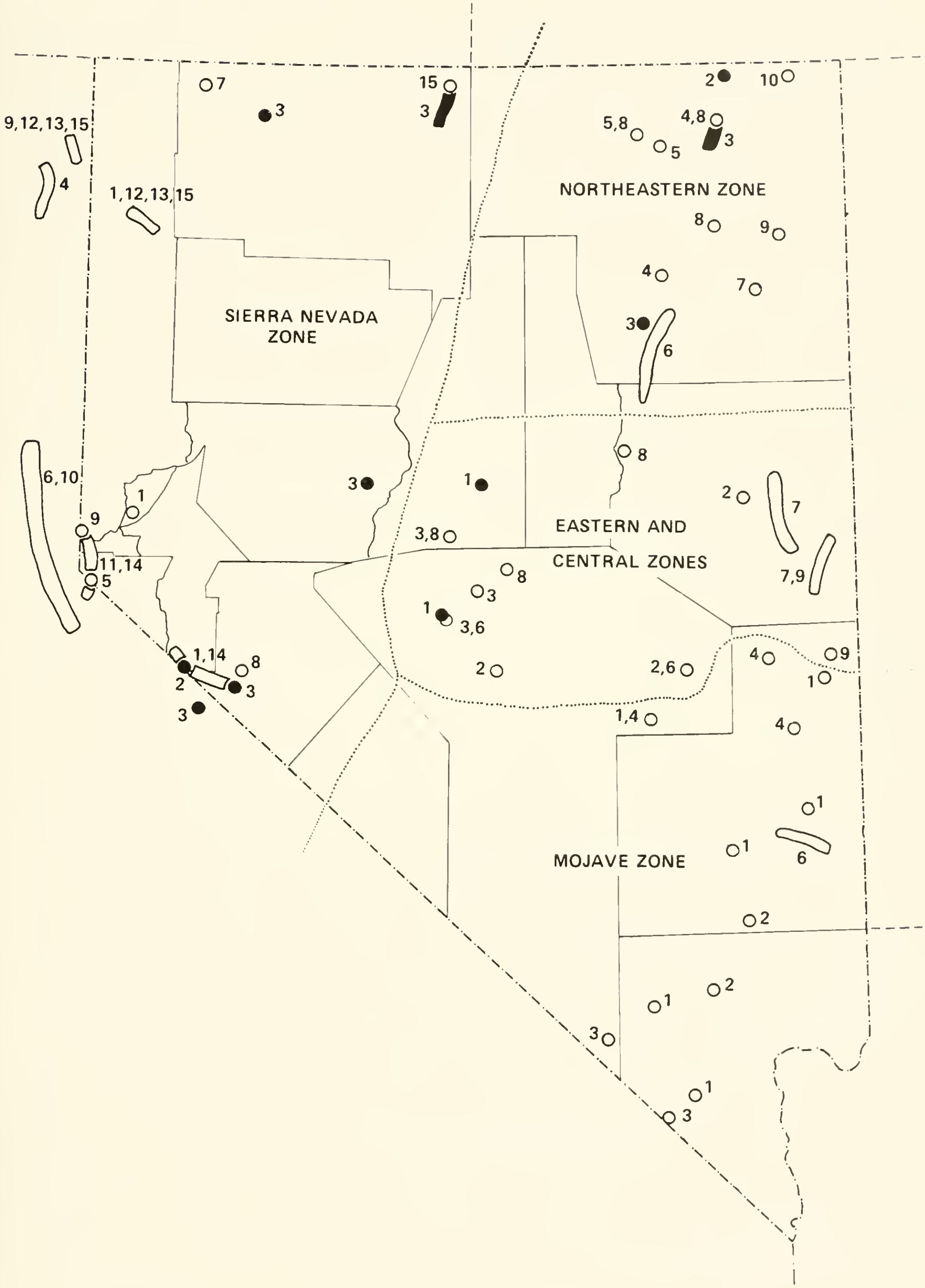
SIERRA NEVADA ZONE
NORTHEASTERN ZONE
EASTERN AND CENTRAL ZONES
MOJAVE ZONE
9,12,13,15
4
1,12,13,15
6,10
1
9
11,14
5
1,14
2
3
8
7
15
10
5,8
4,8
6
7,9
3,8
3,6
2,6
1,4

Fig. 2. Areas of interaction among Great Basin butterflies. Numbers refer to species pairs in Table 4 (Sierra Nevada), Table 5 (northeastern Nevada), Table 6 (eastern and central Nevada), and Table 7 (Mojave). Solid symbols refer to interspecific hybridization; open symbols refer to intraspecific intergradation.

interactions described appear to be sound. Note also that there are some recent records of shifts in the ranges of birds in these same geographic areas of interaction (e.g., Johnson and Johnson 1985).

Pairs of related taxa or segregates are categorized by the type and degree of interaction. In the following sections we discuss areas where subspecies or segregates and closely related species come into contact. A number of closely related species hybridize in these areas. Intergradations between subspecies or segregates include primary intergradations (those between phenotypically similar subspecies or segregates such as those along a cline) and secondary intergradations (those between phenotypically more dissimilar subspecies segregates such as "internal contact" of those from distant points on a ring or *rassenkreis*). Also, in the same geographic areas some species and subspecies (or segregates) exhibit range disjunctions. These zones of allopatry may be geographically wide (such as across the Lahontan Basin) or narrow (between adjacent mountain ranges). Taxa also can be separated by elevation (high and low populations in the same mountain range) or time (flying at different seasons).

Sierra Nevada Zone

Perhaps the most striking element of Great Basin biogeography is the predominance of Rocky Mountain and closely related Great Basin taxa in relative proximity to the east slope of the Sierra Nevada. The occurrence of Sierra Nevada biotic elements east into the Great Basin, conversely, is rare (Behle 1978, Harper et al. 1978, Johnson 1978, Tanner 1978). For instance, in the Snake Range, centrally located in the Great Basin, 54% of 86 species are represented by subspecies that are either shared with the Rocky Mountains or are Great Basin subspecies or segregates most similar to Rocky Mountain taxa. Only 3% of species are of Sierra Nevada affinity. In the Toiyabe Range in the west central Great Basin, 50% of 92 species have Rocky Mountain affinities, while 4% are similar to Sierra Nevada taxa. And, in the White Mountains, just several dozen kilometers from and in direct sight of the Sierra Nevada crest, 34% of 79 species are most similar to Rocky Mountain taxa, and only 17% are of Sierra Nevada affinity.

The east slope of the Sierra Nevada and the adjacent western Great Basin, as a consequence, might be expected to be an area of vigorous interaction among distinguishable butterfly taxa which may have only recently come into contact. This is the single most active area of intergradation for Great Basin birds (Johnson 1978, Johnson and Johnson 1985), and the same appears to be true for butterflies (Table 4). These interactions include many species and involve a wide variety of types and degrees of differentiation and/or disjunct distributions within this geographic area (Fig. 2).

Geographic areas of contact within the Sierra Nevada Zone are generally narrow. Sierran *Speyeria zerene zerene* and a western Great Basin subspecies, *S. z. malcolmi*, for example, intergrade (a primary intergradation) only in the vicinity of Carson City (Moeck 1957, Grey and Moeck 1962). The more widespread Great Basin subspecies, *S. z. gunderi*, intergrades with *S. z. conchyliatus* in the Granite and Warner mountains on the northern Nevada-California border (a secondary intergradation between Rocky Mountain and Sierra Nevada subspecies [Grey and Moeck 1962, Grey 1972]). Two *Speyeria callippe* phenotypes (*S. c. nevadensis* and *S. c.* near *semivirida*) intergrade in this same area. A population of *Neominois ridingsii*, apparently intermediate between *N. r. stretchii* and an as yet undescribed Sierra Nevada segregate, occurs here as well. *Euphydryas anicia wheeleri* and *E. chalcedona macglashanii* produce an apparently intermediate population in the Sweetwater Mountains (Murphy and Ehrlich 1983), while *E. anicia macyi* and *E. a. veazieae* intergrade across a broad area along the Oregon and Nevada border.

The extreme western Great Basin ranges additionally have some Sierra Nevada–derived taxa or segregates which are phenotypically distinct. *Thorybes mexicana blanca* of the White, Wassuk, and Sweetwater mountains and undescribed *Hesperia miriamae* and *Lycaena rubidus* segregates restricted to the White Mountains are examples of populations closely related to Sierra Nevada taxa. The latter appears related to the Sierran subspecies, *L. r. monachensis*, and is replaced elsewhere in the Great Basin by the widespread *L. r. sirius*.

Some species or subspecies (or segregate)

TABLE 4. Taxa pairs of butterflies that show various speciation phenomena in the western Great Basin/east slope Sierra Nevada region (most widespread Great Basin taxon listed before Sierra Nevada or other taxon).

NARROW ZONE OF SYMPATRY AND INTERSPECIFIC HYBRIDIZATION
1. *Mitoura siva chalcosiva* and *M. nelsoni nelsoni*
2. *Euphydryas anicia wheeleri* and *E. chalcedona macglashanii*
3. *Limenitis weidemeyerii latifascia* and *L. lorquini*

NARROW ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:
4. *Hesperia comma harpalus* and *H. comma yosemite*
5. *Anthocharis sara thoosa* and *A. s. stella*
6. *Lycaena arota virginiensis* and *L. a. arota*
7. *Lycaena rubidus sirius* and *L. r. rubidus*
8. *Callophrys sheridanii comstocki* and *C. s. lemberti*
9. *Euphilotes battoides glaucon* and *E. b. battoides* or *E. b. intermedia*
10. *Plebejus icarioides fulla* and *P. i. icarioides*
11. *Speyeria zerene malcolmi* and *S. z. zerene*
12. *Speyeria zerene gunderi* and *S. z. conchyliatus*
13. *Speyeria callippe nevadensis* and *S. c. semivirida*
14. *Phyciodes campestris campestris* and *P. c. montana*
15. *Neominois ridingsii stretchii* and *N. ridingsii* seg.

NARROW ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:
16. *Chlosyne acastus acastus* and *C. palla* seg.
17. *Coenonympha ochracea mono* and *C. ampelos ampelos*

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:
18. *Thorybes mexicana blanca* and *T. mexicana nevada*
19. *Hesperia miriamae* seg. and *H. m. miriamae*
20. *Polites sabuleti genoa* and *P. s. tecumseh* (elevational)
21. *Pontia sisymbrii elivata* and *P. s. sisymbrii*
22. *Euchloe hyantis lotta* and *E. hyantis* ssp.
23. *Lycaena editha nevadensis* and *L. e. editha*
24. *Lycaena rubidus sirius* and *L. rubidus* ssp. (elevational)
25. *Satyrium fuliginosum semiluna* and *S. fuliginosum* ssp.
26. *Satyrium californica* seg. and *S. c. cygnus*
27. *Satyrium sylvinus* seg. and *S. s. sylvinus*
28. *Strymon melinus pudica* and *S. m. setonia*
29. *Glaucopsyche piasus nevada* or *G. p. toxeuma* and *G. p. piasus*
30. *Plebejus melissa melissa* and *P. m. fridayi* or *P. m. paradoxa* (elevational)
31. *Plebejus saepiolus saepiolus* and *P. saepiolus* seg. (elevational)
32. *Plebejus shasta minnehaha* and *P. s. shasta*
33. *Euphydryas editha monoensis* and *P. e. aurilacus* or *P. e. nubigena* (elevational)
34. *Euphydryas anicia wheeleri* and *E. a. veazieae* or *E. a. macyi*
35. *Cercyonis pegala* seg. and *C. p. stephensi*

BROAD ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:
36. *Polites sonora utahensis* and *P. s. sonora*
37. *Speyeria cybele letona* and *S. c. leto*
38. *Speyeria egleis toiyabe* and *S. e. egleis*
39. *Speyeria mormonia artonis* and *S. m. mormonia*

Table 4 continued.

40. *Euphydryas editha lehmani* and *E. e. monoensis*
41. *Coenonympha ochracea mono* and *C. ochraceae brenda*

ALLOCHRONIC SYMPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:
42. *Euphilotes battoides baueri* and *E. b. glaucon*
43. *Euphilotes enoptes ancilla* and *E. e. enoptes*

pairs are narrowly sympatric, or nearly so, with little or no hybridization or intergradation in this zone. The closely related *Chlosyne palla* and *C. acastus* appear to be sympatric at the eastern base of the Sierra Nevada and in the Pine Nut and Virginia mountains without hybridizing. *Anthocharis sara thoosa* and *A. s. stella* co-occur in extreme western Nevada but with little intergradation (these, in fact, may be different species). Another species pair, *Limenitis weidemeyerii* and *L. lorquini*, hybridizes in a very narrow zone just east of the Sierra Nevada (Perkins and Perkins 1967) with extensions northward into Idaho and southwestern Alberta. Yet another pair, *Mitoura siva* and *M. nelsoni*, have long been considered distinct species. They, however, hybridize in a broad region in the western Great Basin and hence may be one species.

Isolated high-elevation populations of at least two species, *Polites sabuleti* and *Phyciodes campestris*, exist in the Sierra Nevada bounded on both the east and west by more widespread, lower-elevation subspecies. Two other species, *Euphydryas editha* and *E. chalcedona*, exist as a series of elevational subspecies (perhaps ecotypes) on the west slope to the crest of the Sierra Nevada and as a single middle-elevation subspecies on the east slope and into the western Great Basin. Numerous Great Basin subspecies (or segregates) are "replaced" by Sierra Nevadan taxa between the western portion of the Great Basin and the crest of the Sierra Nevada (Table 4). There is usually narrow elevational allopatry and/or allochrony (imposed by elevational differences in phenology) between these phenotypes, but intergradation occurs in some. Furthermore, both *Euphilotes enoptes* and *E. battoides* are represented by sympatric allochronic "populations." These distinct univoltine populations fly at single locations at different times of the year and thus thus are reproductively isolated temporally (hence should constitute "allochronic species").

Table 5. Pairs of butterfly taxa showing various speciation phenomena in the northeastern Great Basin (most widespread Great Basin taxon listed first).

Narrow zone of sympatry between closely related species without hybridization.

1. *Euphydryas anicia wheeleri* and *E. colon nevadensis*

Narrow zone of sympatry and interspecific hybridization:

2. *Euphilotes enoptes ancilla* and *E. battoides glaucon*
3. *Coenonympha ochracea brenda* and *C. ampelos elko*

Narrow (usually) zone of sympatry and intergradation between representatives of divergent subspecies:

4. *Colias alexandra edwardsii* and *C. a. astraea*
5. *Plebejus acmon acmon* and *P. a. lutzi*
6. *Speyeria nokomis apacheana* and *S. n. nokomis*
7. *Speyeria egleis utahensis* and *S. e. linda*
8. *Phyciodes campestris campestris* and *P. c. camillus*
9. *Euphydryas editha lehmani* and *E. e. hutchinsi*
10. *Limenitis archippus lahontani* and *L. a. archippus*

Narrow zone of allopatry between closely related species:

11. *Papilio bairdii* and *P. oregonius* (may be conspecific)

Narrow zone of allopatry between representatives of divergent subspecies:

12. *Anthocharis sara thoosa* and *A. sara browningi*
13. *Satyrium sylvinus* seg. and *S. s. putnami*
14. *Euphilotes rita pallescens* and *E. r. mattonii*
15. *Speyeria atlantis greyi* and *S. atlantis elko*

Broad zone of allopatry between representatives of divergent subspecies:

16. *Satyrium saepium provo* and *S. saepium* seg.
17. *Lycaena nivalis browni* and *L. n. nivalis*

Disjunctions between distinct species and between subspecies or segregates within the same species are manifest in both narrow and wide zones of allopatry in the Sierra Nevada Zone (Table 4). Some of these "gaps" are just a few miles wide, such as between the easternmost margin of the Sierra Nevada and the westernmost Great Basin mountain ranges. But other gaps include much of the broad expanse between the eastern Sierra Nevada and the mountains of central Nevada. Many species that range continuously across the region north of the Great Basin are also absent in this same broad area. Note that many gaps in distribution more or less coincide with regions of intergradation and of overlap between pairs of taxa discussed above.

Northeastern Nevada Zone

Another area of substantial apparent incipient speciation in the Great Basin is the northeastern portion of Nevada (Fig. 2). This area should probably include northwestern Utah, southern Idaho, and southeastern Oregon, but for these latter areas few pertinent data exist. Information does exist for much of Elko and Humboldt counties and northern Eureka and Lander counties in Nevada. This area is considerably smaller in extent and lacks the abrupt topographical and ecological discontinuity of the Sierra Nevada–Great Basin interface. Nonetheless, some combination of factors there promotes differentiation and replacement. The region also marks the western or southernmost extent of the distributions of many species in the Great Basin (see below).

Table 6. Pairs of butterflies taxa showing various speciation phenomena in central (C) and eastern (E) Great Basin (the most widespread Great Basin taxon is listed first).

Narrow zone of sympatry and interspecific hybridization:

1. *Plebejus acmon texanus* and *P. lupini lupini* (C)

Narrow zone of sympatry and intergradation between representatives of divergent subspecies:

2. *Pontia sisymbrii elivata* and *P. sisymbrii* seg. (E, C)
3. *Satyrium behrii crossii* and *S. b. behrii* (C)
4. *Celastrina ladon echo* and *C. l. cinerea* (C)
5. *Glaucopsyche piasus nevada* and *G. piasus daunia* (E)
6. *Plebejus acmon texanus* and *P. a. acmon* (C)
7. *Speyeria zerene gunderi* and *S. z. platina* (E)
8. *Phyciodes campestris campestris* and *P. c. camillus* (C)
9. *Limenitis weidemeyerii latifascia* and *L. w. angustifascia* (E)

Narrow zone of allopatry between representatives of divergent subspecies:

10. *Lycaena arota virginiensis* and *L. a. schellbachi* (E)
11. *Euphilotes battoides baueri* and *E. battoides* seg. or *E. battoides* nr. *bernadino* (C)
12. *Euphilotes enoptes ancilla* and *E. enoptes* seg. (C)
13. *Plebejus saepiolus saepiolus* and *P. s. gertschi* (E) (elevational)
14. *Euphydryas editha lehmani* and *E. e. koreti* (E, C) (elevational)
15. *Neominois ridingsii stretchii* and *N. r. dionysus* (C)

As in the Sierra Nevada Zone, there are replacements (specific and subspecific) with or without hybridization or intergradation and some, mostly narrow, allopatries (Table 5). While the zone of interaction along the Sierra Nevada is east/west in orientation, that in northeastern Nevada is more complicated (Fig. 2). The majority of interactions there involve east/west replacements of Rocky Mountain taxa with those of the Great Basin or Sierra Nevada. There are, however, several

TABLE 7. Pairs of butterfly taxa showing various speciation phenomena at the transition between the Great Basin and Mojave Desert (Great Basin taxon listed first).

NARROW ZONE OF SYMPATRY AND INTERGRADATION BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

1. *Pyrgus communis communis* and *P. c. albescens* (partial elevational allopatry, possibly different species)
2. *Hesperopsis libya lena* and *H. l. libya*
3. *Anthocharis cethura cethura* and *A. c. pima*
4. *Mitoura siva chalcosiva* and *M. s. rhodope*
5. *Glaucopsyche lygdamus oro* and *G. lygdamus* seg. (partial elevational allopatry)
6. *Euphydryas anicia wheeleri* and *E. a. alena*
7. *Cercyonis sthenele paulus* and *C. s. masoni*

NARROW ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

8. *Chlosyne acastus acastus* and *C. neumoegeni neumoegeni*

NARROW ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

9. *Polites sabuleti sabuleti* and *P. s. chusca*
10. *Papilio indra nevadensis* and *P. indra martini* or *P. indra* seg.
11. *Euphilotes battoides baueri* and *E. b. martini*
12. *Plebejus melissa melissa* and *P. melissa* seg.
13. *Apodemia mormo mormo* and *P. mormo* seg. (partial elevational and seasonal allopatry)

BROAD ZONE OF ALLOPATRY BETWEEN CLOSELY RELATED SPECIES:

14. *Chlosyne acastus acastus* and *C. palla vallismortis*

BROAD ZONE OF ALLOPATRY BETWEEN REPRESENTATIVES OF DIVERGENT SUBSPECIES:

15. *Plebejus icarioides ardea* and *P. icarioides* seg.
16. *Plebejus shasta minnehaha* and *P. s. charlestonensis*
17. *Speyeria zerene gunderi* or *S. z. malcolmi* and *S. z. carolae*
18. *Euphydryas anicia wheeleri* and *E. a. morandi*
19. *Limenitis archippus lahontani* and *L. a. obsoleta*
20. *Limenitis weidemeyerii latifascia* and *L. w. nevadae*

north/south replacements of taxa from Oregon or Idaho with generally widespread Great Basin taxa. One subspecies each of both *Speyeria egleis* and *S. atlantis* extends into this zone from the north and another from the east (Austin 1983). Furthermore, intergradation of phenotypes occurs among at least seven other subspecies pairs. For some of these (e.g., *Speyeria nokomis*, Swisher and Morrison 1969) this blending occurs over a broad area of the eastern Great Basin and northwestern Colorado; for others (e.g., *Euphydryas editha*) the cline is quite narrow. Finally, hybridization apparently occurs between *Euphilotes battoides* and *E. enoptes* (Shields 1977) and between the semispecies *Coenonympha ampelos* and *C. ochracea* of the *C. tullia* superspecies complex in this area.

Eastern Nevada–Western Utah Zone

This region, which includes White Pine and Lincoln counties in Nevada and parts of adjacent Utah, is a comparatively minor area of speciation and faunal replacement (Table 6, Fig. 2). The apparent subspecific endemics are shown in Table 3. Most phenotypically identifiable replacements consist of Great Basin subspecies or segregate replacing Rocky Mountain subspecies with minor intergradation. There is, in addition, some replacement of desert subspecies or segregates with subspecies or segregates which range widely north of this zone. This portion of the Great Basin is most noteworthy as a northern or western limit of the distributions of a number of taxa (see below).

Central Nevada Zone

This area includes the central Nevada mountains and valleys and is another comparatively minor area of interaction among phenotypes (Table 6, Fig. 2). Many of the interactions discussed for the previous two zones extend for varying distances into the Central Nevada Zone. Both east/west and north/south interactions are involved. A particularly interesting feature in this zone, and in other areas to the north as well, is the apparent hybridization between two species of blues, *Plebejus acmon* and *P. lupini* (Goodpasture 1973). The zone, in part, forms the eastern edge of a broad gap or zone of allopatry between species which are present between here and the Sierra Nevada (see above).

Mojave Desert–Great Basin Zone

This area, including parts of Lincoln, Nye, and Esmeralda counties, Nevada, and Washington County, Utah, is recognized as the northern limit of Mojave Desert plants (Beatley 1975, Meyer 1978) and birds (Behle 1978, Johnson 1978), hence the southern limit of the Great Basin. Mammalian and herpetological distributions also support this as a distinct area of biological discontinuity (Hall 1946, Banta 1965a, b). Several butterfly species occurring widely in both areas exhibit different phenotypes on either side of this transition, while others intergrade across this area (Table 7, Fig. 2). There is a zone of allopatry for some taxa and segregates between the Great Basin and Mojave Desert, but this zone is generally

TABLE 8. Rocky Mountain butterfly species extending west to the Sierra Nevada across the Great Basin.

Hesperopsis libya
Hesperia uncas
Colias alexandra
Lycaena rubidus
Mitoura siva
Speyeria nokomis
Chlosyne acastus
Euphydryas anicia
Limenitis weidemeyerii
Coenonympha ochracea
Neominois ridingsii

narrow. Only for *Limenitis archippus* is there a broad zone of allopatry; several hundred kilometers separate *L. a. obsoleta* in the Colorado River drainage and *L. a. lahontani* along the Humboldt River.

Wasatch Front Zone

The interface of the western escarpment of the Rocky Mountains with the Great Basin in central Utah superficially presents topographical and ecological contrasts comparable to that of the Sierra Nevada zone. Nevertheless, faunal replacement in this zone is not as striking as along the western edge of the Great Basin. Some endemic subspecies (or segregates) occur in this zone, and there is replacement of some Rocky Mountain taxa with those of the Great Basin. A sizable number of Rocky Mountain subspecies as discussed below, however, extend past this area well into the Great Basin. Widespread Great Basin butterflies such as *Hesperia comma harpalus*, *Pontia sisymbrii elivata*, *Euchloe hyantis lotta* (this taxon may be a species in itself, separate from *E. hyantis fide* P. A. Opler), *Lycaena rubidus sirius*, *Plebejus icarioides fulla*, *P. shasta minnehaha*, *Speyeria coronis snyderi*, and *S. callippe harmonia* range west from the Wasatch Front across virtually the entire Great Basin, some as far as the east slope of the Sierra Nevada.

DISTRIBUTIONAL LIMITS

Distributional limits of butterflies in the Great Basin and adjacent areas exhibit repeating patterns of particular interest. Some species, as mentioned, totally avoid the Great Basin, occurring solely at its borders. This overall situation essentially results from four distinct distribution patterns: (1) eastern taxa that occur to the western limits of the Rocky Mountains, (2) extreme western taxa extending no further east than the east slope of the Sierra Nevada, (3) taxa of mainly Rocky Mountain affinity that occur to the eastern borders of the Great Basin, then north across Idaho and Oregon and, in numerous cases, south into the Sierra, and (4) southern taxa that occur north to southern Nevada and/or southwestern Utah.

Other species reach the limits of their ranges somewhere within the Great Basin region. This includes a number of butterfly taxa that enter only the eastern portion of the Great Basin and otherwise possess a distributional pattern like the species in (3) above. The limits of these latter two groups coincide closely with the zone boundaries discussed in the previous section on speciation.

Few Sierra Nevada species extend into the Great Basin and only *Plebejus lupini*, as mentioned above, for a substantial distance. The remainder occur, for the most part, only in the western Great Basin ranges. Of the two apparent endemic species of butterflies in the Sierra Nevada, *Hesperia miriamae* and *Colias behrii*, only *H. miriamae* extends its distribution into the Great Basin as a phenotypically distinct isolate found solely in the White Mountains. Endemic Sierra Nevada subspecies also have made few inroads into the Great Basin. Among the approximately 20 primarily alpine or subalpine taxa, only *Plebejus franklinii podarce* (one record from the Virginia Range) and *Polites sabuleti tecumseh*, *Chlosyne w. whitneyi*, and *Euphydryas editha nubigena* (Sweetwater Mountains) extend east into the Great Basin. The east slope of the Sierra Nevada, in turn, is the western distribution limit of at least 11 Rocky Mountain species (Table 8).

A number of Rocky Mountain species (some of which also occur in the Sierra Nevada) enter the Great Basin only in northeastern Nevada (Table 9). Most of these species have restricted Great Basin distributions and occur in both the Sierra and Rocky Mountains. Numerous additional species occur as isolates on many of the Great Basin ranges.

Three species with primarily southern distributions, *Hesperopsis alpheus*, *Anthocharis cethura*, *Philotiella speciosa*, occur throughout much of the western Great Basin but not the eastern. Several others extend to the east-

TABLE 9. Widespread butterfly species entering the Great Basin only in the northeastern portion.

Hesperia nevada
Parnassius phoebus
Papilio eurymedon
Pieris napi
Lycaena cupreus
Lycaena dorcas
Speyeria cybele
Speyeria atlantis
Speyeria mormonia
Phyciodes tharos

ern and central regions. None, however, reach northeastern Nevada except as strays or nonpermanent populations. A number of species reach their northern distributional limits in southern Nevada, south of the Mojave Desert/Great Basin transition (Austin and Austin 1980). Likewise, numerous Great Basin species have their southern distributional limits near that boundary. Nonetheless, more than 10% of the butterfly species in the Spring Mountains in extreme southern Nevada are of Great Basin affinity, and several endemic subspecies and segregates in this range appear to be closely related to Great Basin taxa (Austin 1981). This suggests a more extensive southern distribution for much of the Great Basin fauna in the past and agrees with our knowledge of the vicissitudes in Pleistocene climate (e.g., Martin and Mehringer 1965, Wells 1983). Taxa with primarily northern distributions (e.g., alpine *Colias, Boloria, Erebia, Oeneis*), on the other hand, contribute very little in general to the Great Basin fauna. However, three putative "species," *Papilio oregonius*, *Euphydryas colon*, and *Coenonympha ampelos* (each conspecific with or siblings of more widespread Great Basin species), enter the northeastern region. One, *C. ampelos*, extends the furthest south, well into western Nevada to the Carson River basin.

PALLIDITY

At least 20 butterfly species exhibit their most pallid phenotype in the Great Basin (Table 10). An additional three butterfly subspecies groups reach their extreme in pallidity in the region. Linsdale (1938) and Hall (1946) noted a similar phenomenon in Nevada birds and mammals. Seven of the pallid butterfly taxa and segregates are restricted to the northeastern region, seven are in western Nevada, three are in central Nevada, and six are more generally distributed. Some pallid subspecies and segregates are extremely restricted geographically, such as *Cercyonis oetus pallescens*, found only in small areas of the Reese River and Big Smoky valleys, and an undescribed *Euphilotes rita* segregate, found only at Sand Mountain east of Fallon. White alkaline or other pale soil was suggested as the key to predator-mediated selection for a pale ground color for many of these species (Emmel and Emmel 1969, 1971, Emmel and Mattoon 1972, Wielgus and Wielgus 1974). This may be true for some nondesert species as well (e.g., Hovanitz 1940, 1941, Bagdonas and Harrington 1979) and is supported by the presence of extreme dark phenotypes of some species in dark-background, marshy areas of the Great Basin (e.g., *Polites sabuleti* in eastern Nevada). The presence of pallid phenotypes in much of the Great Basin, of course, is also consistent with Watt's (1968) findings associating lighter basal wing color with warmer thermal regimes.

TABLE 10. List and general distribution of Great Basin pallid butterfly taxa.

WESTERN GREAT BASIN
Thorybes mexicana blanca
Euphilotes rita seg.
Speyeria zerene malcolmi ("*zerene*" ssp. group)
Speyeria callippe nevadensis ("*nevadensis*" ssp. group)
Coenonympha ochracea mono
Cercyonis pegala stephensi
Neominois ridingsii seg.

CENTRAL GREAT BASIN
Polites sabuleti seg.
Speyeria egleis toiyabe
Cercyonis oetus pallescens

NORTHEASTERN GREAT BASIN
Ochlodes sylvanoides bonnevilla
Lycaena editha nevadensis
Speyeria atlantis greyi
Speyeria atlantis elko ("*irene*" ssp. group)
Speyeria mormonia artonis
Phyciodes campestris seg.
Coenonympha ampelos elko

GENERAL GREAT BASIN
Hesperia uncas lasus
Incisalia eryphon seg.
Speyeria nokomis apacheana
Speyeria zerene gunderi
Limenitis archippus lahontani
Cercyonis sthenele paulus

DISCUSSION

The Great Basin butterfly fauna substantiates many zoogeographic generalities previously drawn for other taxonomic groups, particularly birds, in this region. Foremost, there is a general impoverishment of species richness inward from the peripheries, especially from the Rocky Mountains westward. This would be predicted from the similar distribution patterns recorded for plants (Billings 1978, Harper et al. 1978), in light of the close association of butterflies and their larval host plants. Nevertheless, suitable habitat (including adequate specific host plant availability) appears to exist for many butterfly species missing from portions of the Great Basin.

This impoverishment, as well as the previously noted endemism, presence of "relict" populations, and indications of recent extinctions (Austin 1985), is consistent with an "island effect" (MacArthur and Wilson 1967). This situation in the Great Basin largely arises from the sequestering of biotic diversity in comparatively small and isolated patches of montane habitat surrounded by sagebrush-dominated desert. The insular biogeography, particularly area effects and immigration-extinction dynamics, of the montane Great Basin mammals, birds, and butterflies has been discussed previously (Brown 1971, 1978, Austin 1981, Murphy and Wilcox 1985, Murphy et al. 1986, Wilcox et al. 1986). The same relationships are seen in fish and land snails (Smith 1978, Pratt 1985).

Montane or boreal biotic elements in the Great Basin appear to exhibit relictual distributions. This is best substantiated by mammalian distributions since they include both recent (Brown 1971, 1978) and fossil (Grayson 1982, 1983) evidence. These data indicate that present-day boreal mammalian faunas are not at equilibrium (that is, they lack balanced rates of extinction and of colonization) but are largely the result of range constriction and subsequent extinction (without recolonization) of a once widespread Pleistocene fauna. Fossil evidence from the central Great Basin reinforces the popular view that boreal habitat, extensive in the Pleistocene, withdrew northward and contracted toward montane summits. Grayson (1983) reports the fossil presence of the vole *Phenacomys* cf *intermedius* in the Toquima Range. This species is now restricted to areas far north and west of that range. Furthermore, pika *(Ochotona princeps)* remains have been recovered more than 1,000 m lower in elevation than known at present. Grayson (1982) implies that: (1) boreal mammals were widely distributed across the lowlands, (2) extinction led to the present absence of certain species on certain montane islands, (3) certain species became extinct on all montane islands, and (4) there was no Holocene recolonization.

For butterflies, we have only present-day distributions to examine. Butterflies, like birds, are considerably more vagile than most mammals; thus, it is not surprising that they show less-dramatic effects of island size and isolation. That butterflies are more mobile than mammals (but less so than birds) is reflected in the comparatively low slope associated with the species-area curves for butterflies from Great Basin mountain ranges (Murphy et al. 1986, Wilcox et al. 1986). Hence, rates of interrange (interisland) dispersal should be higher, and recolonization after extinction more frequent, in butterflies than in mammals. Nonetheless, a significant area effect is found for butterflies. But, supporting the notion that rates of extinction exceed that of colonization in at least some butterfly species, Wilcox et al. (1986) have shown that the numbers of "sedentary" butterfly species are better correlated with area than are "vagile" butterflies. Less-mobile taxa (e.g., montane land snails and lowland fish) exhibit an even greater effect of isolation and extinction in this region (Smith 1978, Pratt 1985).

Note that islandlike effects of area and isolation are not restricted to montane or boreal elements in the Great Basin. Lowland riparian butterflies appear to be equally isolated, and the faunas of these communities exhibit similar effects (Austin 1985). Riparian butterfly species richness decreases from the Colorado River Valley northward (upstream) into the central Great Basin. In the northern Great Basin, species richness decreases from the relatively rich upper river valleys (Humboldt, Carson, Walker) downstream toward the central Great Basin.

Given the high number of phenetically distinct, geographically restricted endemic butterfly subspecies and segregates, it is of interest to note patterns of differentiation in other taxa within the Great Basin. Speciation in all taxa is most striking along the western and northeastern edges of the Great Basin. But, differentiation certainly is not limited to these areas. Stutz (1978), for instance, identified several rich evolutionary sites for *Atriplex* in the Great Basin, similar to those found for birds (Behle 1963, Johnson 1978), and corresponding to centers of differentiation and limits of distributions of plants in the Great Basin as outlined by Cronquist et al. (1972). These studies and our butterfly data clearly indicate the existence of distinct areas of interaction and speciation within the whole of the Great Basin.

As we mentioned in several sections above, butterflies and birds are extremely similar in their patterns of distribution and differentiation within the Great Basin. This similarity also extends to other taxa including reptiles and amphibians (Stebbins 1954) and mammals (Hall 1946, Hall and Kelson 1959). *Ambystoma tigrinum* and *Bufo woodhousei* are Rocky Mountain amphibian species not occurring in the Great Basin but extending west along its northern margin. A far-western Great Basin subspecies of *Bufo boreas* replaces a widespread interior subspecies in the western Great Basin, and an isolated subspecies occurs in the Inyo Region. Reptiles that avoid the Great Basin but occur along its borders include *Phrynosoma douglasii* and *Thamnophis sirtalis*, the latter occurring in both the Rocky Mountains and the Sierra Nevada. Subspecific intergradation occurs along the Sierra Nevada–Great Basin interface (*Sceloporus graciosus*, *S. occidentalis*, *Thamnophis elegans*, *Crotalus viridus*) and near the Mojave Desert–Great Basin transition (*Callisaurus draconoides*, *Phrynosoma platyrhinos*, *Uta stansburiana*). Extension of primarily southern species northward in the western Great Basin east of the Sierra Nevada is relatively common. Tanner (1978) commented on the absence in the Great Basin of expected montane species or of endemic species of amphibians and reptiles.

Numerous examples of similar phenomena exist among mammals. Species such as *Lepus americanus*, *Eutamias amoenus*, *Tamiasciurus douglasii*, and *Martes americana* are found in both the Rocky Mountains and Sierra Nevada but not the Great Basin. Others extend northward from the southern deserts only in the western Great Basin. An interface exists between subspecies in the extreme southern or extreme western Great Basin for several mammal species. Subspecific endemics largely follow the patterns described above for butterflies. One species, *Microdipodops pallidus*, in fact, is a Great Basin endemic. The distributions of mammals at the species level (Hagmeier 1966) are consistent with our butterfly data; and more fine-grained, below-the-species-level studies may well further strengthen this comparison with our findings.

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REPRODUCTIVE ECOLOGY OF BLACK-TAILED PRAIRIE DOGS IN MONTANA

Craig J. Knowles[1]

ABSTRACT.—Reproductive ecology of black-tailed prairie dogs (*Cynomys ludovicianus*) was studied on the Charles M. Russell National Wildlife Refuge in northeastern Montana (1978–1980 and 1985). Breeding took place from early March through early April in most years. Persistent snow cover and below normal temperatures in February and March of 1978 delayed the start of breeding. Litter size averaged 4.4 but varied significantly among years. Average yearly litter size was correlated ($r^2 = 0.986$) with summer (June-September) precipitation prior to the breeding season. Largest average yearly litter size (5.0) followed record precipitation, while the smallest average yearly litter size (3.8) followed extreme drought. More than half the yearling females failed to breed while 88% of the females two years and older bred. Testes weights were greatest early in the breeding season and regressed rapidly during April.

Black-tailed prairie dogs (*Cynomys ludovicianus*) occur throughout the Great Plains from southern Canada to Texas within an area of great climatic variation. Such climatic variation may be expected to influence timing of breeding and possibly reproductive potential of prairie dogs. Various aspects of prairie dog reproductive ecology have been studied over a wide geographic region (Wade 1928, Anthony and Foreman 1951, Anthony 1953, King 1955, Koford 1958, Davis 1966, Tileston and Lechleitner 1966, Foreman 1968, Kerwin 1972, Stockrahm 1979, Garrett et al. 1982, Hoogland 1982a, b). Although many of these studies are of one reproductive season or of a single colony, some variation in timing of breeding and number of young is apparent. Breeding in prairie dogs begins as early as late January in Oklahoma (Anthony and Foreman 1951) and as late as mid-March in North Dakota (Stockrahm 1979). Timing of breeding in prairie dogs could not be altered by manipulating temperature and photoperiod in a laboratory (Foreman 1968). Females come into estrus for one day only (Hoogland 1982b), and their gestation period is estimated between 32 and 35 days (Anthony and Foreman 1951, Hoogland 1986). Reports of average *in-utero* litter size have ranged from 4.0 (Smith 1967) to 5.2 (Tyler 1968). My study examined timing of breeding and number of young produced by black-tailed prairie dogs in Montana and sought to determine whether environmental variables might influence these parameters.

METHODS

Prairie dogs were collected at six colonies by shooting in spring of each year from 1978 to 1980 and again in 1985 on the Charles M. Russell National Wildlife Refuge in northeastern Montana (108°30′W, 47°45′N). Collections were timed to obtain pregnant females or females shortly postpartum. Some presampling in March and early April was needed to establish the onset of breeding in 1978 and 1979. The majority of prairie dogs was collected during the second and third weeks of April except in 1978 when many individuals were collected in May.

Sex, weight, and total length were recorded for each prairie dog. Lower mandibles were examined and assigned to one of three age groups based on wear of molariform teeth. These groups and criteria for classification were as follows: (1) light wear, cusps showing little or no wear; Stockrahm (1979) found this wear pattern to be characteristic of yearlings (one to two years old); (2) moderate wear, cusps showing definite wear but still very distinct; and (3) great wear, cusps worn enough to be indistinct. According to Stockrahm (1979), considerable overlap occurs in tooth wear between age classes of prairie dogs over two years; thus, the tooth-wear classes are considered only general indications of age. Numbers of embryos or uterine scars were recorded for each necropsied female. A crown-rump measurement was taken for all embryos from 1978 through 1980 but only for

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TABLE 1. Average crown-rump measurements (mm) and percentage of lactating females by week of collection during April 1978, and the years 1979, 1980, and 1985 combined.

	1978				1979, 1980, 1985			
	Crown-Rump		Percent		Crown-Rump		Percent	
Week	Mean	SD	lactating	N	Mean	SD	lactating	N
1–7					<5		0	2
8–14					27.6	15.8	8	60
15–21	12.0	10.0	0	17	39.9	21.2	23	13
22–28					46.4	12.5	68	22

TABLE 2. Summary of reproductive parameters for female prairie dogs collected on the Charles M. Russell National Wildlife Refuge, Montana.

		Percent	Breeding females		All females	
Year	N	breeding	$\bar{X}$ Embryos	SD	$\bar{X}$ Embryos	SD
1978	47	63	4.4	1.2	2.7	2.3
1979	58	67	5.0	1.4	3.6	2.6
1980	46	74	3.8	0.8	2.8	1.8
1985	39	67	4.1	1.0	2.8	2.2
Total	190	67	4.4	1.2	3.0	2.3

a single embryo of each litter in 1985. Testes were weighed to the nearest 0.1 g for animals collected from 1978 through 1980.

A one-way ANOVA was used to test for variation of litter sizes among years, litter sizes among tooth-wear classes, and weights of males and females among years. Chi-square test of homogeneity was used to test for differences in proportions of breeding females among years and among tooth-wear classes. Differences in weights and lengths between males and females were tested for significance with a Students t-test. Iterative correlation coefficients were calculated to determine the time period prior to breeding that precipitation most closely correlated with yearly average litter size. Similar calculations were also made to determine the relationship of body weight with precipitation for male prairie dogs collected in April. Females were excluded from this analysis because weights of embryos were not subtracted from their body weight.

RESULTS

A total of 367 prairie dogs (198 females, 169 males, $P > 0.10$, $X^2 = 2.292$, 1 d.f.) was collected between 11 March and 27 May. Lactating females were collected as early as 17, 13, and 14 April in 1979, 1980, and 1985, respectively. In 1978 no lactating females were collected up to 21 April, but collections were not resumed until 13 May, at which time lactating females predominated in the collection. Small embryos (less than 5 mm crown-rump) were noted in the collection as late as 19 April 1978, 17 April 1979, 13 April 1980 and 1985. These data suggest that breeding started as early as the second week of March and continued into early April. Breeding appeared to be delayed in 1978 (Table 1). Average crown-rump measurements were smaller for embryos taken during the third week of April in 1978 compared to other years.

The first detected emergence dates for young were 11, 2, and 1 June for 1978, 1979, and 1980, respectively. No comparable observations were available for 1985. An average of 44 days elapsed between earliest parturition date and first emergence date for these years. In 1977 I observed young above ground on 24 May, and S. Olson (personal communication) reported young up on 14 May in 1981, suggesting that breeding may have taken place even earlier during those two years. Variation in timing of breeding among years appeared to be related to temperature and snow cover during February and March. These two months in 1977 and 1981 were extremely mild, with only sporadic snow cover and mean temperatures around 2 C (U.S. Dept. of Commerce, Roy 24 NE). In contrast, total snowfall in the winter of 1978 exceeded 2 m, snow remained on the ground until early April, and the mean temperature was −5 C for those two months. Although mean temperature during February and March 1979 was similar to 1978,

TABLE 3. Comparison of female reproductive parameters by tooth-wear class together with percentage wear-class distribution by year for 181 females.

Tooth-wear class	Percent breeding	Breeding ♀♀		All ♀♀		Wear-class distribution (%)			
		$\bar{X}$ Embryos	SD	$\bar{X}$ Embryos	SD	1978	1979	1980	1985
Light	40	4.7	1.2	1.9	2.4	53	50	44	21
Moderate	85	4.4	1.1	3.8	1.9	30	26	40	56
Great	94	4.2	1.3	3.6	1.9	16	24	16	23

TABLE 4. Percentage of pregnant females examined by year with one or more resorbed embryos together with percentage of embryos resorbed.

Year	N	Percent pregnant resorbing embryos	Percent resorbed embryos
1978	20	30	6.2
1979	21	24	4.6
1980	28	21	5.6
1985	26	23	7.1
Total	95	24	5.9

snowfall was less and the snow melted off earlier; 1980 and 1985 were intermediate to these extremes.

Approximately two-thirds of all females collected had bred. The distribution of breeding females among years was homogeneous ($P > 0.75$, $X^2 = 1.169$, 3 d.f.) (Table 2). Litter size averaged 4.4 (SD ±1.2, range 1–8) but varied among years ($P < 0.005$, $F = 7.4$, 127 d.f.) (Table 2). Average yearly litter size ranged from 5.0 in 1979 to 3.8 in 1980. Record precipitation occurred in 1978 (57.1 cm), while drought conditions existed on the study area in 1979 and 1980 (27.6 and 22.2 cm for 1979 and 1980, respectively, U.S. Dept. of Commerce, Roy 24 NE). Average litter size was best correlated with summer (June–September) precipitation of the previous year ($r^2 = 0.986$) but showed little correlation with late-fall/winter (November–March) precipitation ($r^2 = 0.004$). Number of embryos produced by all females averaged 3.0 and showed less variation among years than did average yearly litter size (embryos/breeding female).

The distribution of breeding females was not homogeneous among tooth-wear classes ($P < 0.005$, $X^2 = 48.620$, 2 d.f.) (Table 3). Only 40% of the females showing light tooth wear had bred. Among the females showing great tooth wear, 94% had bred. Average litter size did not vary ($P > 0.25$, $F = 0.9$, 119 d.f.) among tooth-wear classes, although there was a tendency for younger animals to have larger litters. However, because of low pregnancy rate, the average number of embryos per female in the light tooth-wear class was only about half that of the other two wear classes.

Evidence of post-implantation mortality (resorption) was found each year. Resorbing embryos were found in nearly a quarter of the pregnant females (Table 4), and 5.9% of the embryos were lost. Of the 23 pregnant females found to be resorbing embryos, only two were resorbing more than one. In 1985 one female was resorbing all three embryos, and another was resorbing two of three embryos.

Average total length of males ($\bar{X} = 383.7$, SD ±26.3 mm) was greater ($P < 0.001$, $t = 5.966$, 356 d.f.) than that for females ($\bar{X} = 369.0$, SD ±20.4 mm). However, no difference was noted ($P > 0.50$, $t = 0.415$, 283 d.f.) in average weight of females ($\bar{X} = 810.8$, SD ±145.0 g) and males ($\bar{X} = 803.5$, SD ±146.4 g) collected during April. This may be accounted for by the fact that many females were pregnant at the time of collection. Weights of both females and males taken during April varied among years (females, $P < 0.05$, $F = 3.1$, 166 d.f.; males, $P > 0.05$, $F = 2.4$, 117 d.f.). Weights of males were most closely correlated ($r^2 = 0.627$) with precipitation from June through October of the previous year.

Average testes weight was greatest during March ($\bar{X} = 3.45$, SD ± 2.32 g, N = 12) and declined through April ($\bar{X} = 0.59$, SD ± 0.42 g, N = 93) and May ($\bar{X} = 0.38$, SD ± 0.26 g, N = 18). Of the five male prairie dogs collected during the month of March that were assigned to the light tooth-wear class, only two had testes weights exceeding 1.0 g. Testes weights of older males collected during this month averaged 5.0 g, suggesting that many younger males may not participate in breeding. Testes of nearly all males collected in April were held abdominally.

DISCUSSION

Timing of breeding in prairie dogs has been variously reported to take place from January through March and appears to occur later with increasing latitude (Johnson 1927, Wade 1928, Anthony and Foreman 1951, King 1955, Koford 1958, Davis 1966, Tileston and Lechleitner 1966, Tyler 1968, Stockrahm 1979). Breeding took place over an extended period from early March to early April during this study. King (1955) and Tileston and Lechleitner (1966) noted that breeding occurred over a one- to two-week period. Although Foreman (1968) found that timing of breeding in female black-tailed prairie dogs could not be altered by manipulating temperature and photoperiod, it was apparent in my study that prairie dogs bred later in 1978 as a result of persistent snow cover during March of that year. Time between birth and emergence of young has been estimated at 56 days by Anthony and Foreman (1951), 45 days by King (1955), 32 to 39 days by Tileston and Lechleitner (1966), and 43.4 days by Hoogland (1986).

Litter size varied considerably among years and appeared to be influenced by precipitation from the previous year, which may also influence body weight of prairie dogs in April. Reproductive failure has been reported to occur in Townsend's ground squirrels (*Spermophilus townsendii*) under drought conditions in Idaho (BLM, U.S. Dept. Interior 1979). Reports of average *in-utero* litter size range from 4.0 to 5.2 (Johnson 1927, Wade 1928, Anthony and Foreman 1951, Koford 1958, Tileston and Lechleitner 1966, Tyler 1968) with no apparent geographical trend. The influence of yearly climatic conditions on litter size may account for this.

Despite the varying climatic conditions during this study and the resulting wide range in average litter size among years, the proportion of females breeding among years remained fairly constant with about two-thirds of the females breeding each year. Wade (1928) reported breeding in 74% of 68 female prairie dogs, and Anthony and Foreman (1951) found 73% of 15 wild-caught females to have bred. My data show that only 40% of the light tooth-wear class (i.e., yearlings) females had bred, whereas most of the females in the two older age classes had bred. King (1955) reported no breeding by yearling females, and Tileston and Lechleitner (1966) found only one breeding yearling female. During another segment of my study involving live trapping and marking (Knowles 1982), I did not document breeding of yearlings in 27 cases in two colonies over two breeding seasons. However, Koford (1958) reported about one-third of the yearling females he collected in Colorado had bred. Stockrahm (1979) found the majority of yearlings in two colonies bred, but in two other colonies very few bred. Garrett et al. (1982) found breeding in yearlings to vary between colonies and years. Evidently breeding in yearling females is highly variable.

Resorption of embryos was a common occurrence each year. Despite some variation among years in both percent of females resorbing embryos and the percent post-implantation mortality, this did not appear to be related to environmental factors. Anthony and Foreman (1951) found evidence of resorption in 3 of 13 (23%) pregnant females and suggested that resorption in prairie dogs may be common.

Testes of most males were in regression at least two weeks before the breeding season terminated. Anthony (1953) found peak testes weight to correspond with the beginning of estrus in females and that regression of accessory sex glands lagged behind the testes, suggesting that males are capable of breeding as long as mobile sperm are present. My data indicated that many yearling males may not attain sexual maturity. Anthony (1953) found that young raised in a laboratory attained sexual maturity a month after older adults. Yearling males were reported not to participate in breeding in a study conducted by Hoogland (1982a).

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FIELD CLINIC PROCEDURES FOR DIAGNOSIS OF *ECHINOCOCCUS GRANULOSUS* IN DOGS[1]

Ferron L. Andersen[2] and M. John Ramsay[3]

ABSTRACT.—*Echinococcus granulosus* is the causative parasite of hydatid disease in humans and represents a significant public health problem within endemic foci in all major continents of the world. This report gives a detailed set of instructions whereby four trained individuals can examine 15–20 dogs per hour for the presence of this organism. The procedure permits the baseline determination of the prevalence of this parasite within any specific population of dogs and also allows the periodic examination of the same animals to determine if recommended preventive and control measures for hydatid disease are being followed by sheep and dog owners in any region where the parasite is known to occur.

Echinococcus granulosus is an extremely small tapeworm (4–6 mm in length; Fig. 1) that lives in the small intestine of dogs and a few related carnivores (e.g., coyotes and wolves). Eggs from the fully developed tapeworm are passed out with the fecal material from the carnivore host. Sheep (and a variety of other domestic and wild animals such as cattle, pigs, deer, and moose) may ingest vegetation contaminated with the carnivore host feces containing these tapeworm eggs. Once the eggs have been ingested by these animals (intermediate hosts), the tapeworm eggs hatch in the duodenum, penetrate through the intestinal lining, and pass via the bloodstream to such filtering organs as the liver or lungs. There the hatched eggs undergo development to the larval stage (termed hydatid cysts; Fig. 2) and become filled with watery (hydatid) fluid. The hydatid cysts continue to grow inside these animals, and tiny microscopic tapeworm heads (termed protoscolices; Fig. 3) develop inside the cysts by extensive asexual reproduction. Once an animal is infected with these hydatid cysts, it has them for the remainder of its life. When that animal dies or is killed, the viscera with the hydatid cysts may be eaten by a dog or other carnivore. The protoscolices are then liberated from the cyst, attach to the intestinal lining of the carnivore, and develop to the tapeworm stage (Schantz 1982). The life cycle of *E. granulosus* is given in Figure 4.

Developmental time in the dog after it eats viscera containing hydatid cysts from an infected sheep until mature tapeworms can be found in the dog's intestine is about 35 days (Thompson 1986). Developmental time in the sheep after it ingests vegetation contaminated with fecal material from the dog containing tapeworm eggs until mature hydatid cysts with protoscolices can be found in the sheep viscera is approximately one year (Schantz 1982).

People who work in close association with dogs and sheep that harbor this tapeworm are also at some risk of contacting the parasite. If such individuals inadvertently ingest some of the tapeworm eggs passed from an infected dog (either from petting or handling the dog or from ingesting food or drink contaminated with dog feces), hydatid cysts may eventually develop within the internal organs of that person. Such an infected person is said to have hydatid disease or echinococcosis. The cysts will continue to grow and develop and may become so large as to interfere with the normal functioning of the particular organ (liver, lung, etc.) in which the cysts are located. Although there are several chemical compounds that will effectively retard the growth of hydatid cysts in humans, there are no compounds that will remove or eliminate the cyst entirely. Consequently, the cysts must on occasion be removed through surgery. Such an operation is naturally very serious, depending

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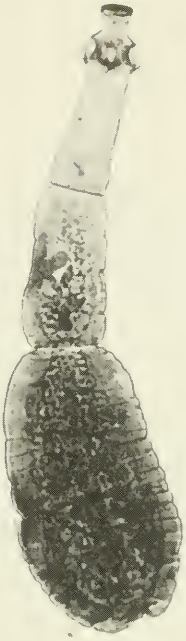

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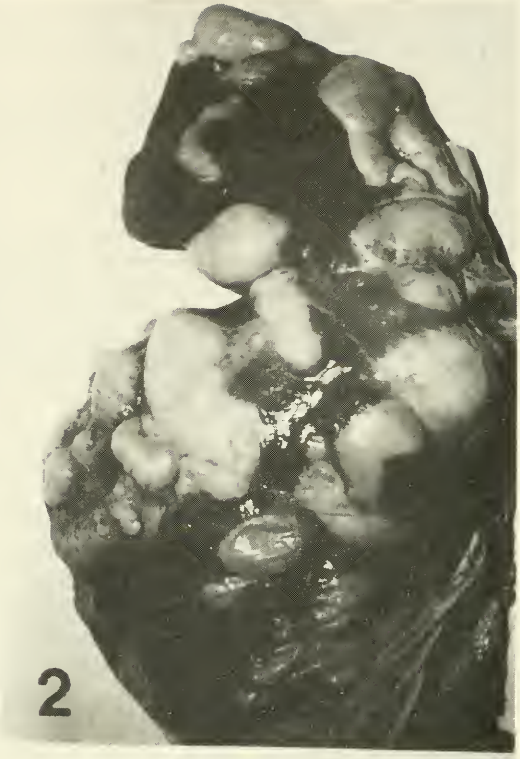

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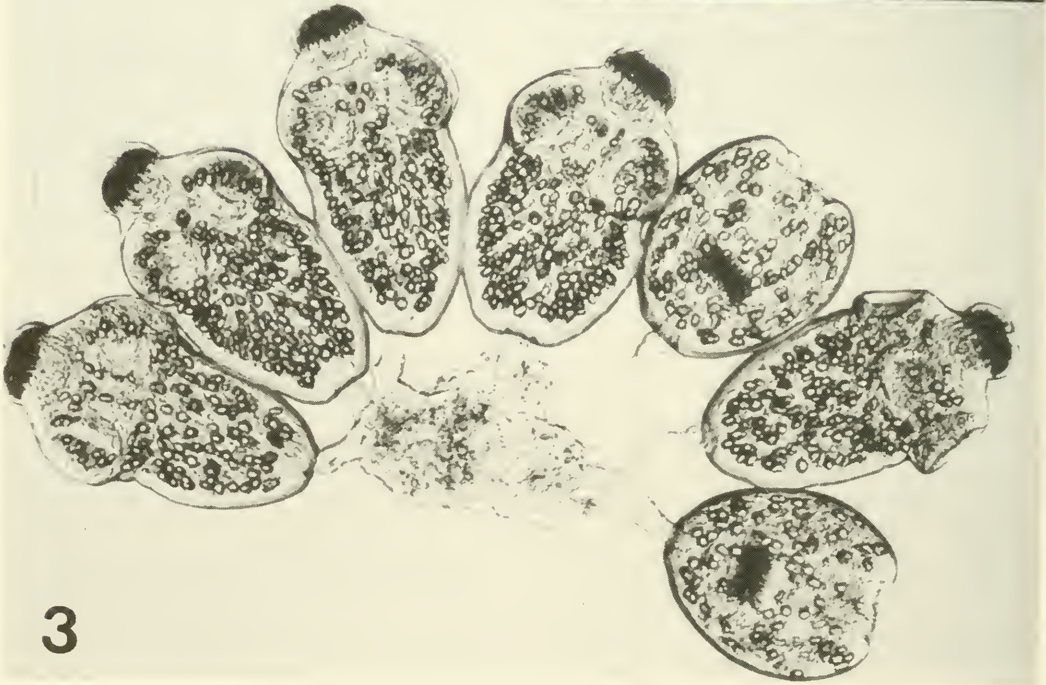

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Fig. 1. Adult *Echinococcus granulosus* tapeworm from an infected dog.
Fig. 2. Hydatid cysts in liver from an infected sheep.
Fig. 3. Protoscolices from a hydatid cyst.

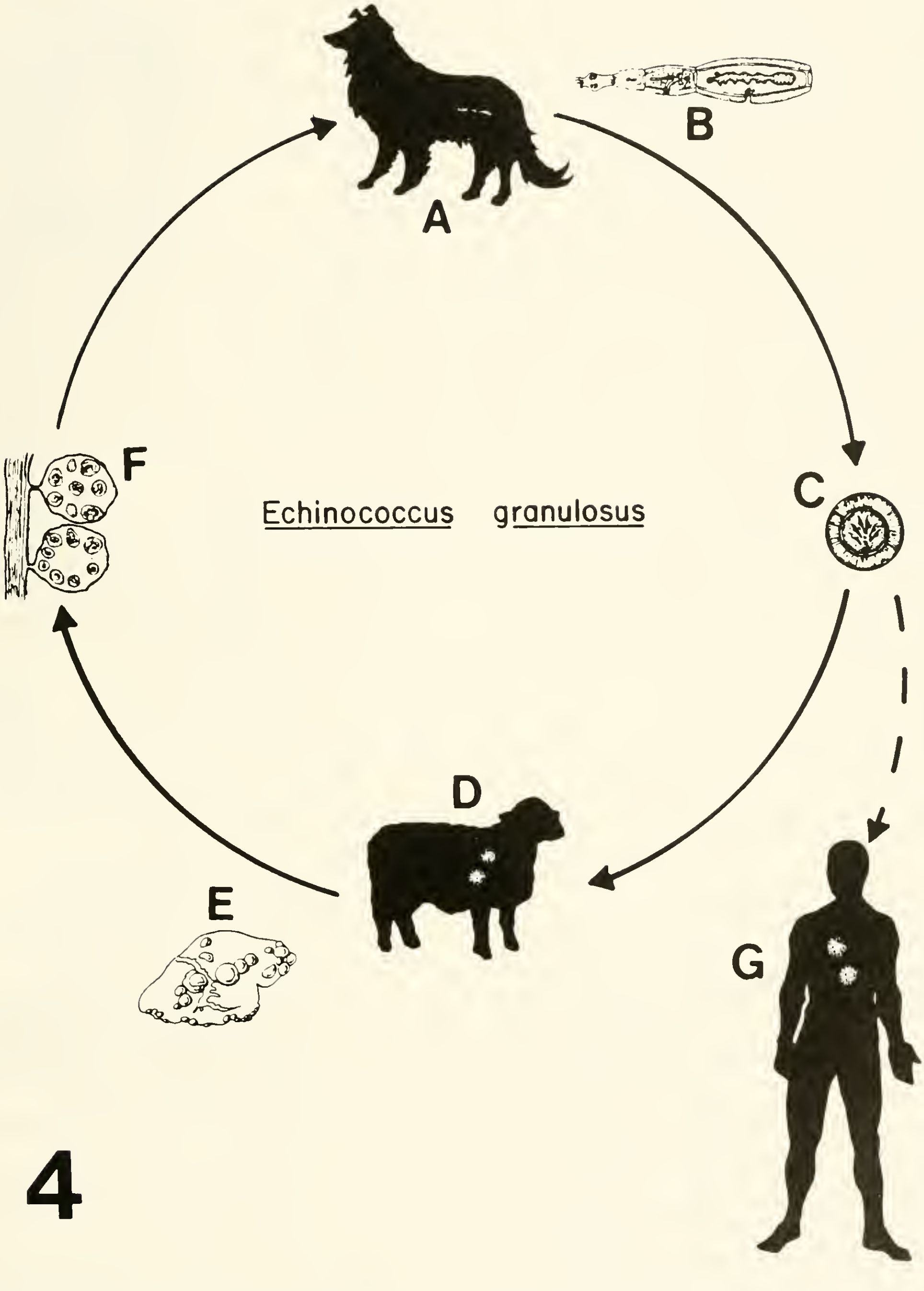

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Fig. 4. Life cycle of *Echinococcus granulosus:* A, Dog (carnivore host) infected with *Echinococcus granulosus* tapeworm in small intestine; this animal becomes infected after eating viscera of sheep (or a related animal) containing hydatid cysts; B, Adult *Echinococcus granulosus* tapeworm (4–6 mm) in small intestine of dog; C, Tapeworm egg (30–40 μ) passed in feces from an infected dog; D, Sheep (intermediate host) with hydatid cysts in viscera; this animal becomes infected after ingesting vegetation contaminated with dog feces containing tapeworm eggs; E, Hydatid cysts in viscera of sheep; F, Tissue section through hydatid cyst with daughter cysts and numerous protoscolices (tiny tapeworm heads); G, Human with hydatid cysts in liver and lung; people become infected after ingesting food or drink contaminated with dog feces containing tapeworm eggs, or by handling or playing with infected dogs.

upon the size and specific location of the developing cyst(s), and in rare cases it may be fatal (Schantz 1982).

At the present time hydatid disease is known to be endemic in parts of Europe, Asia, Africa, South and Central America, New Zealand, and Tasmania. Although the disease is relatively rare in North America, known endemic foci do exist in such places as Alaska, Utah, Arizona, New Mexico, and the Central Valley of California (Gemmell 1979, Andersen 1986).

In many countries of the world where hydatid disease is known to be a significant problem, surveillance studies are routinely done to determine the prevalence of *Echinococcus granulosus* in people, sheep, and dogs (Barbour et al. 1978, Condie et al. 1981, Andersen et al. 1986). Data for the prevalence of hydatid cysts in people come mainly from a survey of hospital records. Data for the prevalence of hydatid cysts in sheep are obtained most often from records at slaughter houses or from a survey of sheep owners who may have observed hydatid cysts in sheep they have killed. However, information on the prevalence of *E. granulosus* tapeworms in dogs is more difficult to obtain. As stated above, these particular tapeworms are extremely small and are not seen by the dog owner or even by the veterinarian at routine inspections. They can, however, be detected by a very thorough examination of the intestinal contents after the dog is killed. This works well for examining dogs suspected of harboring this parasite if the dogs are either strays or not needed as working dogs. Obviously, many of the dogs in an agricultural region are required as working dogs for the sheep industry and, as such, cannot be killed; yet these dogs are the very ones that most likely will be infected with this particular tapeworm. In those cases, the prevalence of *E. granulosus* may be determined through using purgation techniques—i.e., use of a strong laxative (Gemmell 1973, Schantz 1973). Such a procedure not only allows the determination of baseline data on this parasite within dogs living in a specific region, but it also allows the periodic examination of the same animals to determine if recommended preventive and control measures for this disease are being followed by sheep and dog owners in that area. Sheep ranchers must do all they can to prevent dogs from having access to viscera of any infected sheep that might die at their farmstead or range. Specifically, they must not purposefully feed sheep viscera to dogs when the sheep are butchered for mutton (Andersen et al. 1983).

MATERIALS AND METHODS FOR PURGING DOGS

The following information is designed as a set of recommended instructions for purging dogs at a field clinic in a rural community where sheep raising is an important part of agriculture. The specific protocol described requires four trained individuals and is designed to allow the examination of approximately 15–20 dogs per hour.

A. Initial organization.

1. Obtain all necessary approvals from local health officers who may need to be involved or give sanction to the clinic.
2. Advertise details of the clinic through:
    a. any local newspapers;
    b. personal letters to dog or sheep owners where feasible;
    c. announcements sent to schools, churches, or community centers;
    d. posters displayed at local stores or community centers.
3. Details should include:
    a. nature of hydatid disease;
    b. its public health significance;
    c. exact location, date, and time of field clinic;
    d. instructions to dog owners to:
        (1) withhold all food from their dog for 12 hr before the examination (water should be continually available, however);
        (2) bring each dog with a sturdy leash;
        (3) be prepared to sign a "release of responsibility" form for the examination team.
4. Select a site for the clinic somewhat removed from any residential area, playground, public school, or major traffic region. The area where the dogs are to be tied should be relatively free of tall grass, bushes, and any other objects that would inhibit the eventual collection of purged fecal samples. Generally, it is best to avoid the use of

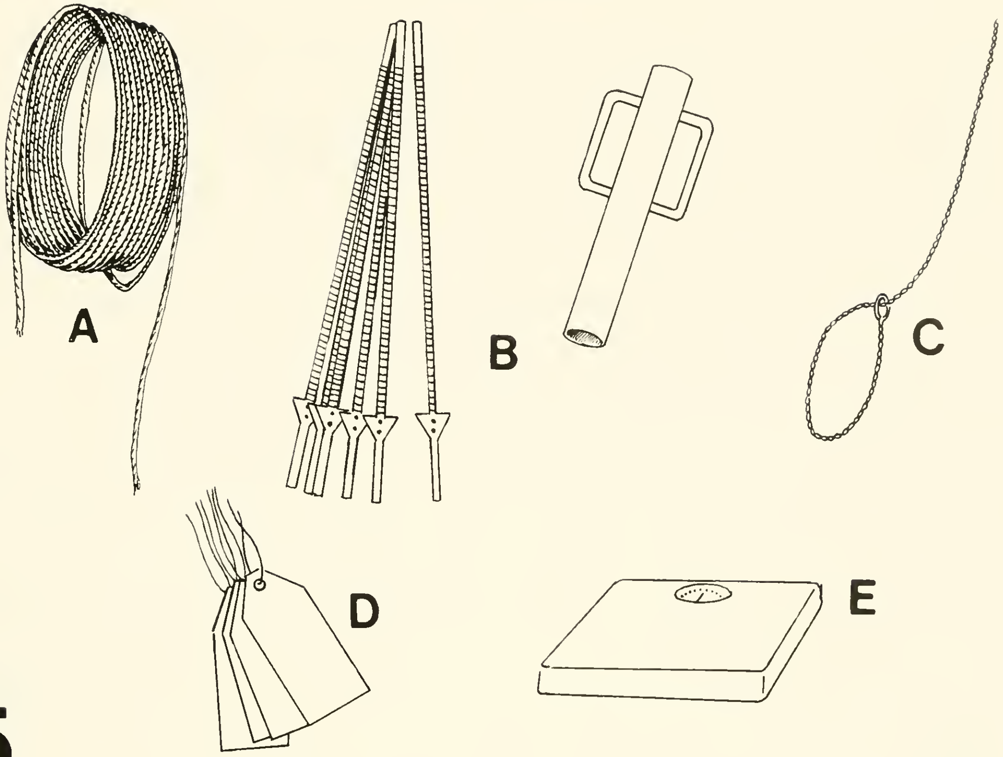

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Fig. 5. Materials for dosing line: A, Long, sturdy rope; B, Metal stakes and stake driver; C, "Choke chain" type leash; D, Identification tags; E, Scales.

cement foundations, paved lots, or even graveled roads. A relatively firm soil substrate nearly free of vegetation seems to be the best type location for a field clinic.

B. Preparation on day of clinic.

1. All members of the examining team should arrive at the clinic site in sufficient time to be completely organized before owners start to bring dogs for examination. The four members of the team should be assigned to separate duties:
   a. No. 1 interviews owners and registers all dogs.
   b. No. 2 administers all purgative medicine.
   c. No. 3 collects all purged samples.
   d. No. 4 examines all samples.
2. A good sturdy fence which dogs cannot jump over or climb through is the best place to tie the individual dogs. If a good fence is not available, a temporary "dosing line" can be constructed with metal posts and a long, heavy rope. Dogs can be tied about 2.5 m apart on a very short leash. This will minimize fighting among the dogs and will lessen any confusion as to which fecal samples belong to which dog. The rope, stakes, stake driver, leashes, individual tags, and scales are shown in Figure 5.
3. All members of the examination team should wear protective clothing (Fig. 6), with the exception of the individual who is assigned to interview the dog owners. That person should not wear a mask or use gloves so that he or she can communicate easily with those who attend the clinics and can also handle all records and educational aids. The wearing of protective clothing serves to protect the members of the examination team and also emphasizes to those who attend the clinic the potential seriousness of hydatid disease.

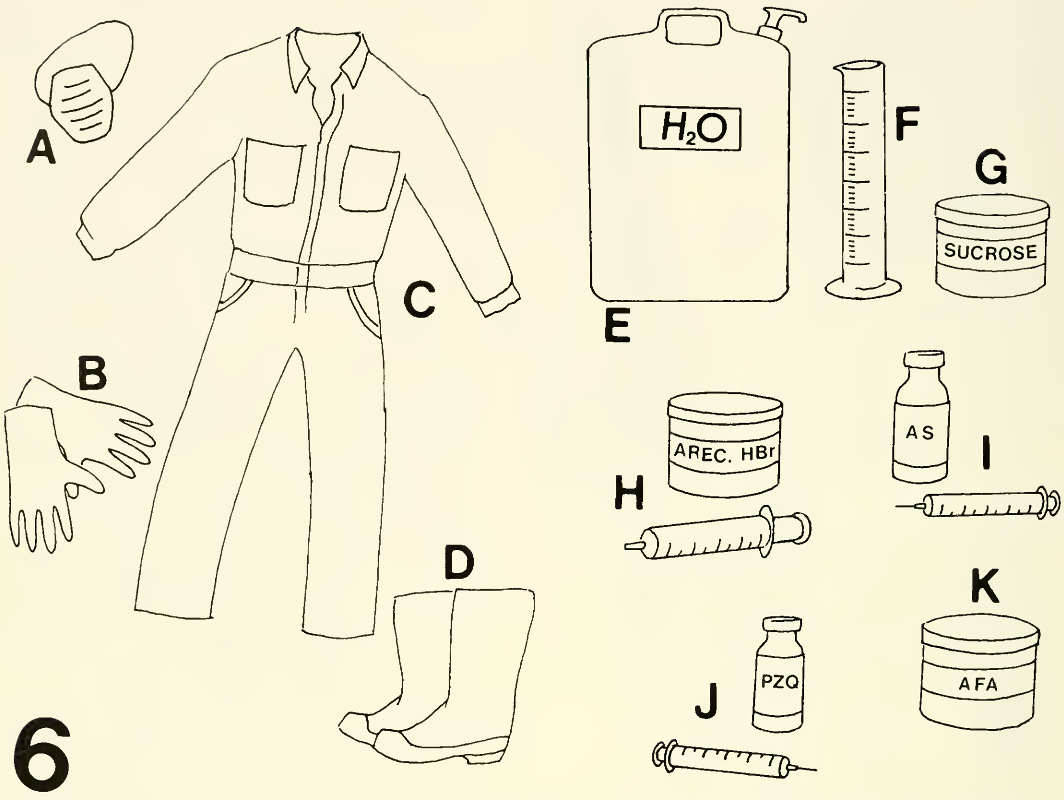

Fig. 6. Protective clothing, chemicals, drugs, and miscellaneous solutions: A, Face mask; B, Latex disposable gloves; C, Coveralls; D, Boots; E, Water container; F, Graduated cylinder; G, Sucrose; H, Arecoline HBr (purgative) and syringe without needle; I, Atropine sulfate (antidote) and syringe with needle; J, Praziquantel (therapeutic drug) and syringe with needle; K, AFA tapeworm preservative solution.

4. A disposal pit into which collected fecal material and disposable items and supplies can be placed should be dug in close proximity to the examination site. The pit needs to be about the size and depth of a regular 30-gal garbage can. If a disposal pit cannot be dug at the clinic site, a large garbage can fitted with a sturdy plastic liner should be available.

C. **Registration of dogs.**

1. As the dogs arrive, one member of the examining team is assigned to greet and interview each owner to obtain the following information:
   a. name and address of dog owner;
   b. name, age, sex, breed, any identifying features, and weight of dog (owner can hold dog on scales and then subtract own weight without dog);
   c. history of the dog's use in agriculture, including answers to the following questions:
      (1) Does dog have contact with sheep?
      (2) Does owner have sheep? If so, how many?
      (3) Does owner allow dog to eat sheep viscera?
      (4) Has dog been treated within the past year for tapeworms?
2. Owner is requested to read and sign a "release of responsibility" form (Fig. 7) that releases all members of the examination team from any and all financial obligation should the dog be injured or die as a result of the purgation or subsequent treatment.
3. Owner is then given educational aids concerning the nature and transmissi-

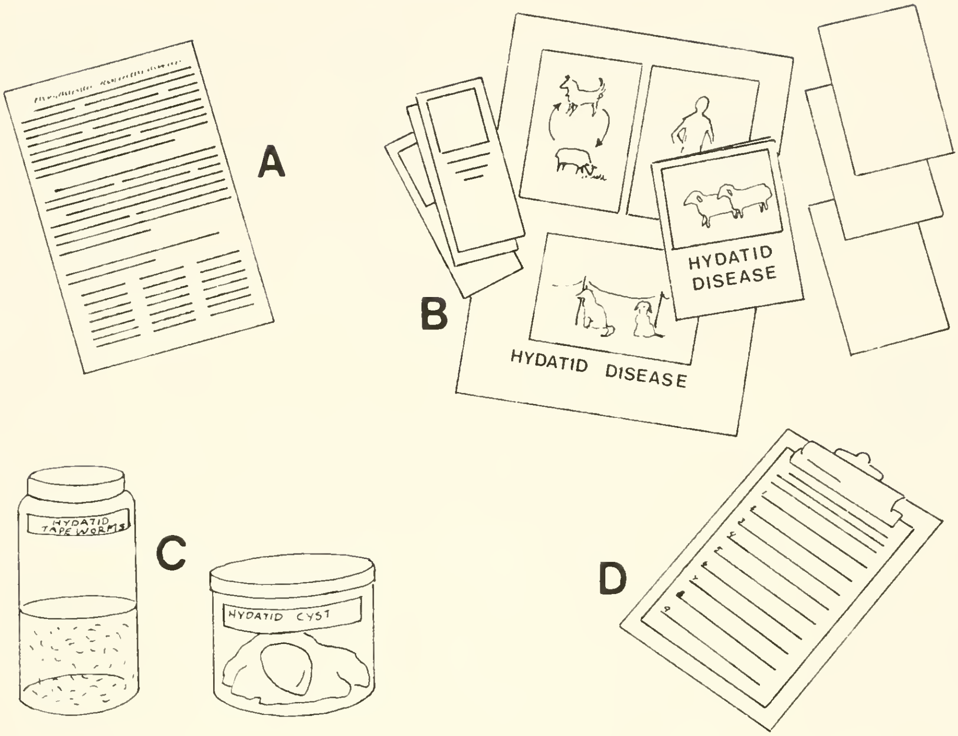

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Fig. 7. Registration forms, educational materials, and survey record sheets: A, Registration data form (top portion), release of responsibility statement (middle portion), results of examination for all dogs belonging to one owner (bottom portion); B, Educational materials for those who attend clinic; C, Preserved specimens of *Echinococcus granulosus* tapeworms from an infected dog and hydatid cysts from an infected sheep; D, Clipboard and record sheets for all dogs examined at the clinic.

bility of hydatid disease and is shown the sample of preserved *Echinococcus granulosus* tapeworms from an infected dog and the sample of a preserved hydatid cyst from an infected sheep (Fig. 7).

4. The dog is then taken to the dosing line where it is individually tethered (Fig. 8). An identification number is given to each dog as it is entered onto the line, and that number is placed on all registration forms and the master list for that particular clinic.

D. Administration of the purgative solution.

1. Arecoline HBr is the purgative agent used and should be premixed as follows: 1.5 g of drug added to 100 ml of water (Fig. 6). Also, sucrose (about 15 g) is added as a sweetener to remove the unpleasant, bitter taste of the compound. The addition of a sweetener is especially important if the dog might need to receive more than one dose on the day of the clinic or if it will be brought back to another clinic at a later date.
2. A veterinarian or one specifically trained individual on the examining team should be assigned to administer all purging medicine at any one clinic. If a dog is tame and manageable, this person can probably give the purgative without help from an assistant (Fig. 9A). If, however, the dog is somewhat unmanageable, it is best for the owner or another member of the team to hold the dog firmly as shown in Figure 9B while the first person administers the drug. Arecoline HBr is administered at a dosage level of 1 ml/4.5 kg (10 lbs) of body weight. The drug should be quickly deposited at the back of the tongue to facilitate swallowing. The mouth of the dog is quickly closed, the

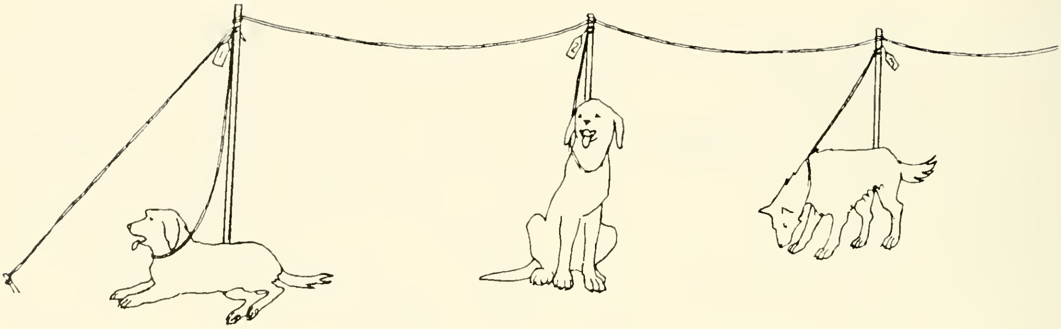

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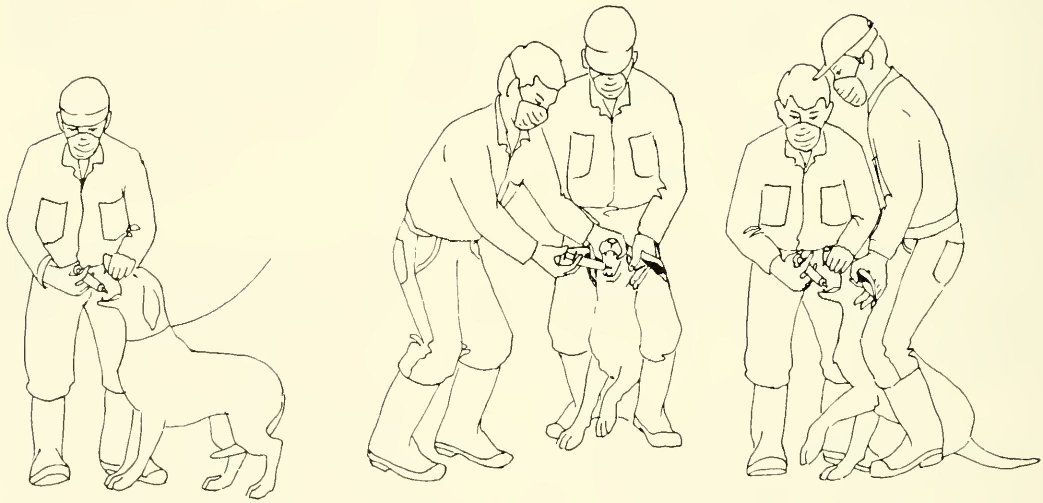
Fig. 8. Dogs individually tethered to dosing line.



9A

9B

Fig. 9. Illustration of purging technique: A, One-man procedure for manageable dogs; B, Two-man procedure for unmanageable dogs.

muzzle elevated somewhat, and the attendant should make sure that the dog swallows the entire dosage amount. If an unmanageable dog is restrained by the owner or second assistant, that person *must not* release the head of the dog until the person administering the drug has pulled away from the dog's mouth. Every effort should be made to handle the dogs gently but firmly. Tight restraint should be used only when necessary, and a good practicing veterinarian should be able to dose most of the dogs single-handedly.

3. The time when each dog receives arecoline is recorded on the identification tag and also entered onto the individual registration form. Shortly after the compound is administered, most dogs will begin to salivate heavily and will also usually vomit. This material should be collected readily and dis-

carded into the disposal pit or garbage container. Some dogs may show moderate to severe reactions to the arecoline HBr and may exhibit marked distress, cardiac excitation, convulsion, and collapse. Generally, such reactions are only temporary. In persistent cases, however, the veterinarian (or person in charge of dosing with arecoline) must be prepared to administer an antidote of atropine sulfate. This is given intramuscularly or subcutaneously at a dose rate of 0.05 to 0.1 mg/kg (Fig. 6). This antidote should allow the dog to recover rapidly; however, it will also probably stop the purgation reflex and that particular dog will then need to be released from the dosing line without further examination. Pups under four months, extremely old dogs, and pregnant or lactating female dogs should probably not be purged (Andersen 1986). In addition, it has been our experience in holding clinics in central Utah over the past 15 years that the small "toy breeds" are likely to show adverse reactions to an arecoline purge.

E. **Collection and examination of purged samples.**

1. In most circumstances when the purgation process proceeds normally, the dog will first void solid to semi-solid fecal material. Since this portion rarely contains parasites, it should be collected from the ground immediately and discarded. After a short delay the second purged material should be a much more liquified portion with small to moderate amounts of mucus present. This portion (especially any mucus) should be carefully picked from the soil substrate with a tongue depressor and transferred to a labeled collecting cup. It is helpful if one attendant holds the dog by the leash to one side while the other attendant collects the purged sample. Additional purged amounts may be passed from the dog while it is tied to the dosing line. This material may be collected and examined also if time is available and if the examiner is not satisfied with previous collections.
2. If, after approximately 30 minutes following administration of the arecoline HBr, a particular dog has not purged and shows no signs of inner peristaltic distress, the attendant might exercise the dog with a short walk in the vicinity of the dosing line. Some dogs are extremely reluctant to defecate while being tethered, and the exercise might be an added stimulus to the purgation process.

   If after 45 minutes or so there has been no purgation whatsoever, the attendant veterinarian might elect to give a second purge (about one-half the initial level). In very rare instances, even a third dose might be given if the veterinarian deems the dog to be in sufficient health and constitution to withstand such a regimen.
3. When a good sample with mucus is passed, one attendant carefully collects the material, labels the collecting cup, and takes the container to a central location for examination (Fig. 10). To minimize any record-keeping errors and to maintain consistency in examination procedures, one member of the team is assigned to do all examination for that particular clinic.
4. Several ml of tap water are added to the collecting cup from a squeeze bottle, and the material is carefully poured into a shallow black-bottom pan for examination. The attendant carefully separates the collected sample with a teasing needle and methodically examines the material with a gentle swirling motion of the pan. The examination should be done in ample lighting, which gives a good color contrast of the tiny white tapeworms against the black background of the examination pan. In cases where objects are difficult to differentiate, the object in question can be viewed under a hand lens or transferred with a medicine dropper to a petri dish and examined in greater detail under a dissecting microscope (Fig. 6). Extreme care must be taken to obtain adequate purged samples and then view them with consistency to locate

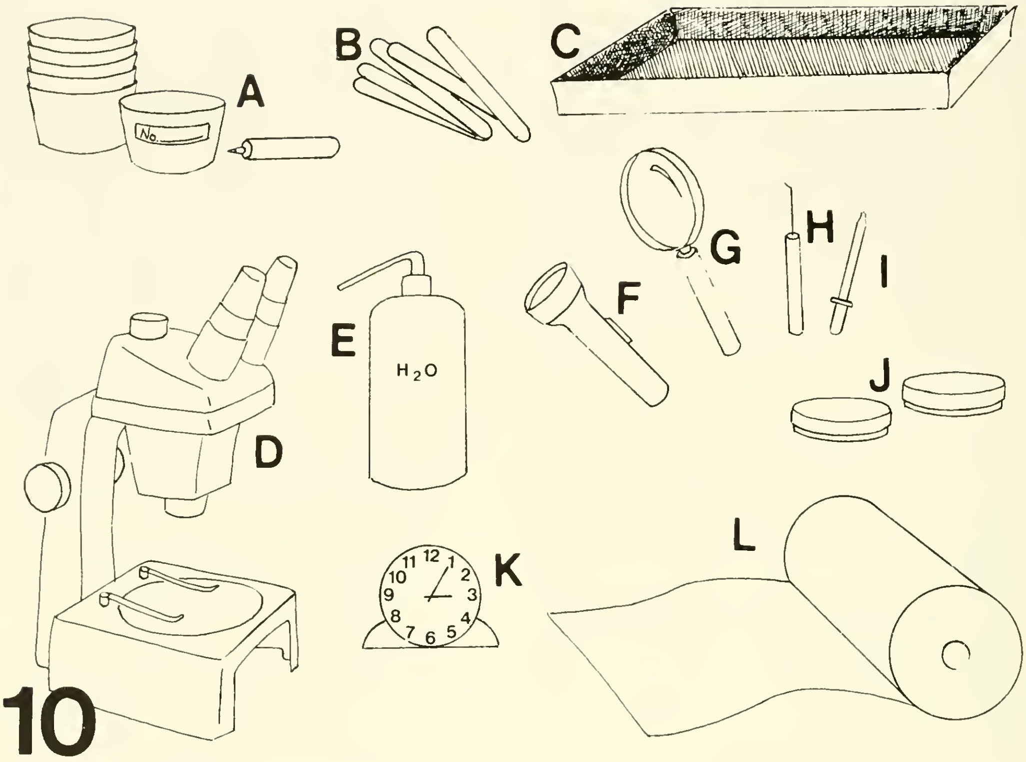


Fig. 10. Examination supplies: A, Collecting cups and marker; B, Tongue depressors; C, Shallow black-bottom examination pan; D, Dissecting microscope; E, Water squeeze bottle; F, Flashlight; G, Hand lens; H, Teasing needle; I, Medicine dropper; J, Petri dishes; K, Clock; L, Roll of paper.

the tiny worms if indeed they are present. Care must also be taken to avoid misidentification of tiny white objects that might have an overall shape similar to the *Echinococcus* tapeworms. Broken or isolated scolices (tapeworm heads) or single proglottids (tapeworm segments) are extremely difficult to detect and differentiate from extraneous materials of similar size and shape.

5. The results are recorded for each dog on the individual registration form and also on the master record for that day's clinic. A record should be kept of:
   a. the quality of the purge (i.e., good, fair, poor);
   b. presence of other worms (i.e., ascarids, large taeniids, etc.; these can be preserved and identified at a later time if that is part of the project protocol since such information is helpful in assessing the eating habits of the dogs);
   c. presence of *Echinococcus granulosus.*

F. Anthelmintic treatment.

1. Any dog shown to be infected with *Echinococcus granulosus* must be treated before the dog is taken from the dosing line. Injectable praziquantel (PZQ) at a dose level of 5 mg/kg is recommended (Andersen et al. 1978). If the program is so designed, all dogs brought to the clinic (irrespective of whether or not they are found to harbor tapeworms) can be treated with the tapeworm medication (Fig. 6).
2. All treatment given should also be noted on the individual registration forms.

G. Removal of dogs from dosing line.

1. As soon as a particular dog is finished, it should be removed from the dosing line, all purged fecal material should be collected and discarded, and a new dog entered onto that site on the dosing

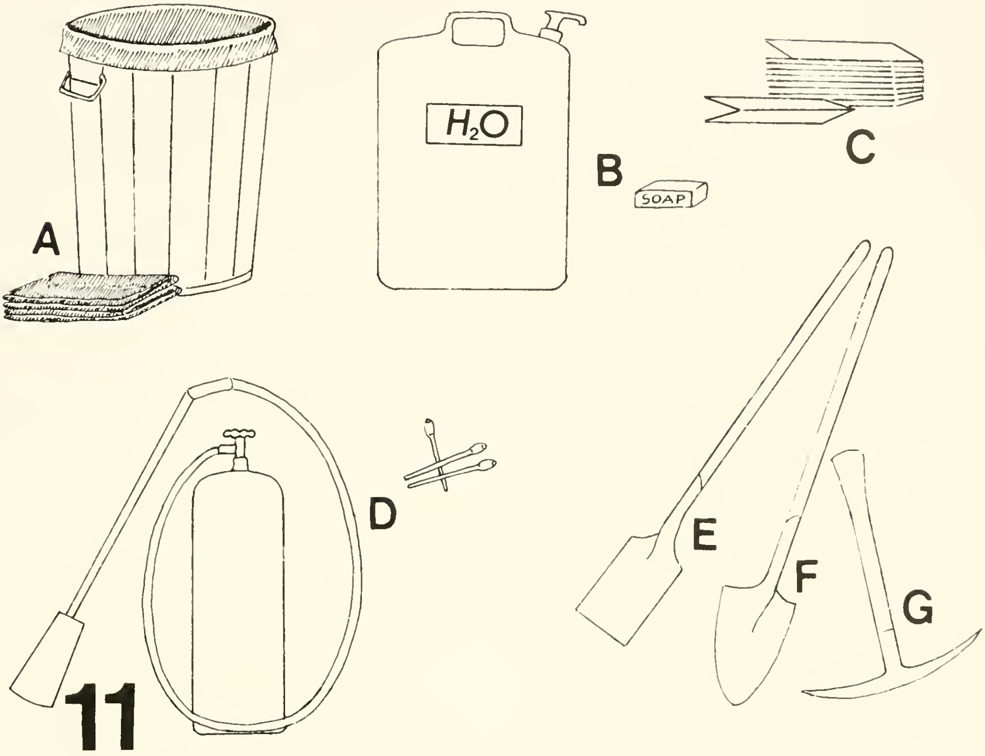


Fig. 11. Clean-up materials: A, Garbage can and plastic liners; B, Water and hand soap; C, Paper towels; D, Propane burner and matches; E, Flat-bladed shovel; F, Round-bladed shovel; G, Hand pick.

line. Dogs that are removed may have rather soiled hindquarters and may need to be cleaned somewhat before leaving the area. It is important to keep the animal as clean as possible while it is on the dosing line and not to permit it to lie down in purged material. Since the dog may purge additional amounts after it has left the clinic site, and since any tapeworm eggs passed from a treated animal are probably not killed by praziquantel (Thakur et al. 1979), it is important that the dogs not be confined near the family home for one to two days following purgation. Owners should also be told of the significance of the results of the examination and be allowed to ask questions concerning the clinic. Members of the examining team should avoid using technical words not understood by dog owners or by other interested individuals who attend these field clinics.

H. Clean-up at clinic site.

1. Figure 11 shows the materials and supplies necessary for proper clean-up following the field clinic. After all dogs have been removed from the dosing line, all fecal material remaining should be collected with a flat-bladed shovel and discarded in the disposal pit or garbage container. A propane weed-burner or flame-thrower is then used to heat the area where the dogs have been tethered. Shovels and other equipment used by clinic personnel can be washed clean over the disposal pit and then flamed with the burner as well. If a temporary dosing line has been used, the rope should be recoiled without allowing it to get in the dirt, and the stakes should be carefully removed and reloaded into the team vehicle.
2. The individual assigned to keep all registration forms and all records should not wear gloves or mask during the

clinic and should refrain from handling any potentially contaminated material. This individual should be responsible for putting away all records, visual aids, and all other materials that have not been handled by those individuals wearing gloves at the clinic.

3. Coveralls should be removed and placed in a plastic bag and should not be worn again without first being boiled in water. Gloves and masks should be discarded, and all team members should wash their hands carefully with soap and water and dry with disposable paper toweling. All other disposable items from the clinic should be discarded into the disposal pit, which should then be covered with an adequate amount of soil to prevent any dogs (or children) from digging into the buried material. If a large garbage can is used instead of a disposal pit, the plastic liner should be tied securely and then eventually incinerated or buried at another site. It is virtually impossible to describe each step of precaution that should be taken by the examination team, but each member should be expressly concerned about his or her own safety as well as that of the other members of the team.

Discussion

Arecoline HBr is a drug manufactured originally from the areca nut which was used by the ancient Chinese for removal of intestinal worms. It was first used against tapeworms in dogs in 1921 (Schantz 1973). However, with the advent of newer, more effective anthelmintics, the use of arecoline HBr in dogs has recently been limited to that of a diagnostic compound. The drug first causes the tapeworms to relax and lose their attachment to the intestinal mucosa; it then causes a marked contraction of the intestinal smooth muscles of the dog (Munday and Smith 1972). This results in an expulsion (purgation) of some or many of the intestinal worms in an infected animals. The compound is known to remove about 90% of all tapeworms present in infected dogs in less than one hour after administration, about half of the ascarid worms, but none of the hookworms (Batham 1946).

Arecoline is used today in many parts of the world in areas where hydatid disease is known to occur as an integral part of preventive and control programs in which purging of dogs for detection of any *Echinococcus* tapeworms present is coupled with health education, control of livestock slaughtering, and improved management of high-risk dogs (Schantz 1982). In central Utah the use of arecoline in field clinics has aided in the overall decrease of *Echinococcus* in infected dogs from a prevalence of 28.3% in 1971 (Andersen et al. 1983) to 2.3% in 1984 (Andersen et al. 1986). This decrease substantiates the benefit of incorporating arecoline purging into a control program for hydatid disease. Dog owners can see first hand if their dogs are indeed infected with these important parasites, which then gives immediate reinforcement to the overall program. Unfortunately, in one study in central Utah 92.5% of the dog owners surveyed knew the cause of hydatid disease and how the parasite was transmitted, 90% of them knew someone who had had surgical removal of hydatid cysts, and yet nearly half of the respondents indicated they still allowed their dogs to sometimes eat part of the sheep carcass following routine butchering on their premises or in the fields (Schantz and Andersen 1980).

An important additional point for workers to remember where arecoline is used as a purging agent in dogs is that varied adverse effects such as tremors, difficulty in breathing, incoordination, and possible collapse can sometimes occur in dogs given this compound (Forbes and Whitten 1961). Also, some owners have complained that their dogs have been definitely weakened and were unable to work in the livestock industry for at least one day following purgation (Batham 1946).

As discussed earlier, the actual examination for the tiny *Echinococcus* tapeworms is very difficult and is best left to experienced individuals. Otherwise, false negative results may be recorded that would lead to improper confidence in the particular control program. In *Echinococcus* diagnostic field clinics, the use of arecoline in the hands of less-than-capable individuals may not only be useless but may even be dangerous if not carried out by experienced personnel and in a standardized manner (Schantz 1982).

In summary, the use of diagnostic field clinics for detection of *Echinococcus* tapeworms is best coupled with an intensive educational effort and with improved management programs by all sheep and dog owners living in endemic regions (Crellin et al. 1982). Following the initial determination of baseline data on the prevalence of *Echinococcus* tapeworms, periodic clinics thereafter with these same high-risk sheep dogs will provide the necessary index of progress which health authorities need to continue direction of successful campaigns in endemic regions.

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SEED GERMINATION CHARACTERISTICS OF *CHRYSOTHAMNUS NAUSEOSUS* SSP. *VIRIDULUS* (ASTEREAE, ASTERACEAE)

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Abstract.—Rubber rabbitbrush (*Chrysothamnus nauseosus* [Pallas] Britt. ssp. *viridulus*) may prove to be a source of high-quality cis-isoprene rubber, but its establishment is limited by a lack of information on seed germination. Consequently, seeds were germinated at alternating temperatures (5–15, 5–25, 15–25, and 20–30 C) in light and dark as well as constant temperatures (15–40 C with 5-C increments) to determine temperature response. Seeds were also germinated in solutions of polyethylene glycol 6000 (0 to −5 bar), salinity regimes (1, 17, 51, and 86 mM) at all the above-mentioned temperatures to determine salinity and temperature interaction. The hormones GA_3 (0, 2.9. 29.0, and 58.0 um) and kinetin (0, 4.7, 23.5, and 47.0 um) were used to study their effect on overcoming salt- and temperature-induced germination inhibition. Seeds of *C. nauseosus* ssp. *viridulus* were very sensitive to low temperature. Best germination was achieved at 25 and 30 C, but these seeds also germinated at a higher temperature (35 C). The seeds of rabbitbrush germinated at both constant and alternating temperatures. Light appears to play little or no role in controlling germination of the seeds of rubber rabbitbrush. However, seeds of rabbitbrush were sensitive to salinity, and seed germination was progressively inhibited by increase in salt concentration, although a few seeds still germinated at the highest saline level. Progressively higher concentrations of polyethylene glycol also progressively inhibited germination. Suppression of seed germination induced by high salt concentrations and high temperatures can be partially alleviated by the application of either GA_3 or kinetin.

Chrysothamnus nauseosus (Pallas) Britt. ssp. *viridulus* (Hall) Hall & Clements is the largest and most robust of the approximately 20 subspecies of *C. nauseosus* (rubber rabbitbrush) (Hall and Clements 1923, Anderson 1966). Anderson (1986a) has reduced *C. nauseosus* ssp. *viridulus* to a variety of *C. nauseosus* ssp. *consimilis*. In this report we have chosen to maintain it at the subspecies level because several characteristics such as higher rubber content (Ostler et al. 1985), size, habitat, and distribution distinguish it from ssp. *consimilis*.

Rubber rabbitbrush as a species occurs widely west of the one hundredth meridian in North America, barely extending from the United States north into Canada and south into Mexico. Rubber rabbitbrush is usually 30–230 cm in height, having several erect stems from the base and with moderately flexible leafy branchlets (McArthur et al. 1979a, McMinn 1980). Subspecies *viridulus*, however, may grow to 3 m in height in the alkaline valleys of west central Nevada and eastern California.

The several subspecies of this perennial shrub show considerable variation in distribution and adaptation (Hall and Clements 1923, McArthur et al. 1979a, Anderson 1986b), in phenolic plant chemistry and palatability to browsing animals (Hanks et al. 1975), in relation to gall-forming insects (McArthur et al. 1979b, Wangberg 1981, McArthur 1986), in seed-germination characteristics (McArthur, Jorgensen, and Weber, unpublished), and in rubber and resin content (Hall and Goodspeed 1919, Ostler et al. 1986, Weber, McArthur, and Hagerhorst, unpublished). The potential of this taxon for rubber production was first suggested by Hall and Goodspeed (1919) and has recently been rated as promising by Ostler et al. (1986). Results of nuclear magnetic resonance analyses demonstrate that Chrysil, the rubber from rabbitbrush, is a high-quality cis-isoprene molecule type rubber. It may be that the rubber production from guayule (*Parthenium argentatum*) and rubber rabbitbrush, both composite family shrubs, could be processed through the same industrial plant. Rabbitbrush is adapted to a wide range of soils including those that are alkaline and to temper-

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Table 1. Effect of NaCl and alternating temperatures on the percent of germination of *Chrysothamnus nauseosus* ssp. *viridulus* seeds in light.

NaCl	Alternating temperatures (C)			
(mM)	5–15	5–25	15–25*	20–30*
0	53.3^{a}	67.8^{a}	90.0^{a}	94.4^{a}
17	49.2^{a}	46.6^{b}	80.0^{b}	79.8^{b}
51*	35.1^{a}	34.0^{bc}	40.2^{c}	53.2^{c}
86*	12.0^{b}	12.0^{c}	35.9^{c}	18.62^{3}

[abcd]Values with the same letter in a column are not significantly different as determined by the Duncan multiple-range test at α .05.

*Two-way analysis of variance indicates (1) NaCl inhibitory above 17 mM, and (2) alternating temperatures (15–25 and 20–30 C) are stimulatory.

Table 2. Effect of NaCl and alternating temperatures on the percent of germination of *Chrysothamnus nauseosus* ssp. *viridulus* seeds in dark.

NaCl	Alternating temperatures (C)			
(mM)	5–15	5–25	15–25*	20–30*
0	54.5^{a}	54.5^{a}	91.8^{a}	96.3^{a}
17	57.2^{a}	53.2^{a}	83.8^{a}	73.2^{b}
51**	33.3^{b}	26.6^{b}	42.6^{c}	54.5^{c}
86**	16.0^{b}	9.3^{c}	34.6^{c}	27.9^{d}

[abcd]Values with the same letter in a column are not significantly different as determined by the Duncan multiple-range test at α .05.

*Two-way analysis of variance indicates (1) NaCl inhibitory above 17 mM, and (2) alternating temperatures (15–25 and 20–30 C) are stimulatory.

ate climates, whereas guayule grows in frost-free or nearly frost-free areas (Johnson and Hinman 1980). Rubber rabbitbrush accessions have up to 6.5% rubber content (Hall and Goodspeed 1919, Ostler et al. 1986, Weber, McArthur, Hagerhorst, unpublished) and will resprout when tops are harvested (Young et al. 1984).

Additional information will be required on germination of rubber rabbitbrush seed if it is to be used as a commercial crop for rubber production. Obtaining young rabbitbrush plants by rooting fresh cuttings is difficult (Everett et al. 1978). Transplanting nursery seedlings is a reliable method, but direct seeding should be more economical. However, direct seeding methods have received little study. Stevens et al. (1981) reported that *C. nauseosus* seed germination declines from 80 to 14% from the second through the fifth year of warehouse storage. In another report, Stevens et al. (1986) demonstrated the importance of proper seed placement in the soil for germination and seedling vigor. Deitschman et al. (1974) reported that eight collections of *C. nauseosus* had an average of 63% seed viability. Sabo et al. (1979) reported a maximum germination of 76% for *C. nauseosus* ssp. *consimilis*.

Our objective was to investigate effects of simulated environmental factors and growth regulators on germination characteristics of rabbitbrush accession with high rubber yield potential to obtain more information on seed physiology. This information could be useful in growing plants from seeds.

Materials and Methods

Seeds of *Chrysothamnus nauseosus* (Pallas) Britt. ssp. *viridulus* were collected in the fall of 1984 from plants growing at Palmetto, Esmeralda Co., Nevada (collected by McArthur, Weber, and Sanderson). This population has large plants up to 3 m in height. Seeds were separated from inflorescences and stored at 4 C in paper bags. Germination tests were carried out in 9-cm-diameter glass petri dishes containing Whatman No. 1 filter paper moistened with 5 ml of distilled water or other test solutions. Three replicates of 25 randomly selected seeds each were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle.

To determine the effect of temperature on germination, we used growth chambers to obtain alternating regimes of 5–15, 5–25, 15–25, and 20–30 C based on a 24-hour cycle, where the higher temperature (15, 25, and 30 C) coincided with a 12-hour light period, and the lower temperature (5, 15, and 20 C) coincided with the dark period. Seeds were also germinated under constant temperatures ranging in 5-C increments from 15 to 40 C. The petri dishes were randomized at each temperature regime. We studied the light requirement by comparing germination in petri dishes in the dark (covered in a box) with germination in petri dishes in the light. Seeds were germinated in distilled water, 17, 51, and 86 mM NaCl solution under the above-mentioned temperature regimes.

Water stress was imposed by adding polyethylene glycol (PEG-6000) to distilled water to give a wide range of osmotic potential (from 0 to −0.5 mpa) (Michel and Kaufman 1973). Several concentrations of GA_3 (0, 2.9, 29.0, and 58.0 um), and kinetin (0, 4.7, 23.5, and 47.0 um) were applied. We recorded germination every day for three days and calculated the rate of germination using an index of

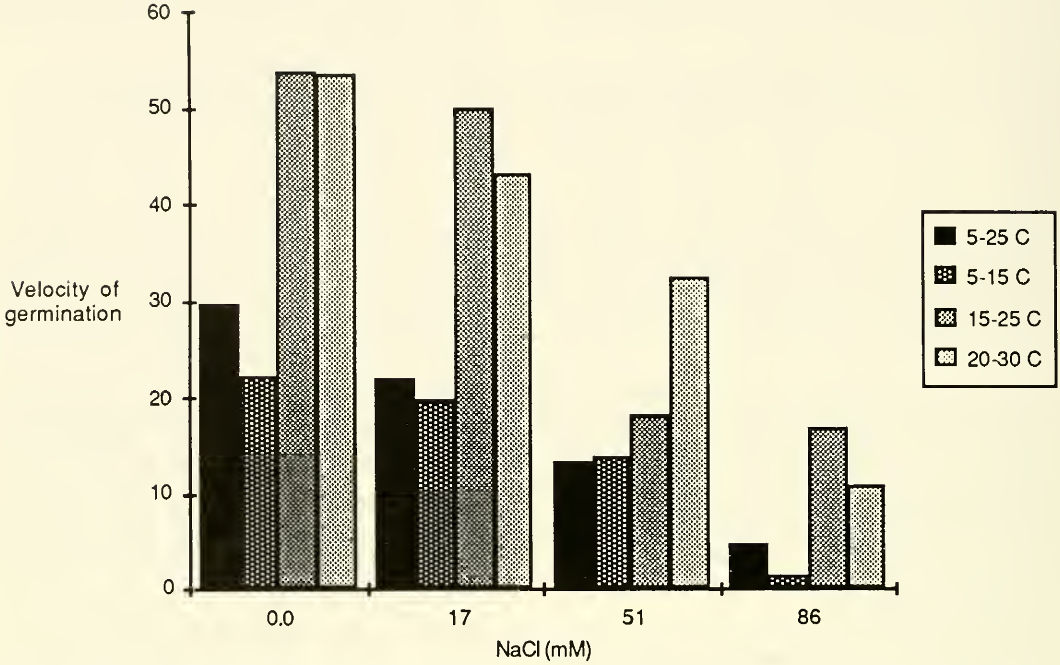

Fig. 1. Rate of germination (velocity of germination) of seeds of *Chrysothamnus nauseosus* ssp. *viridulus* at alternating temperatures and three concentrations of NaCl.

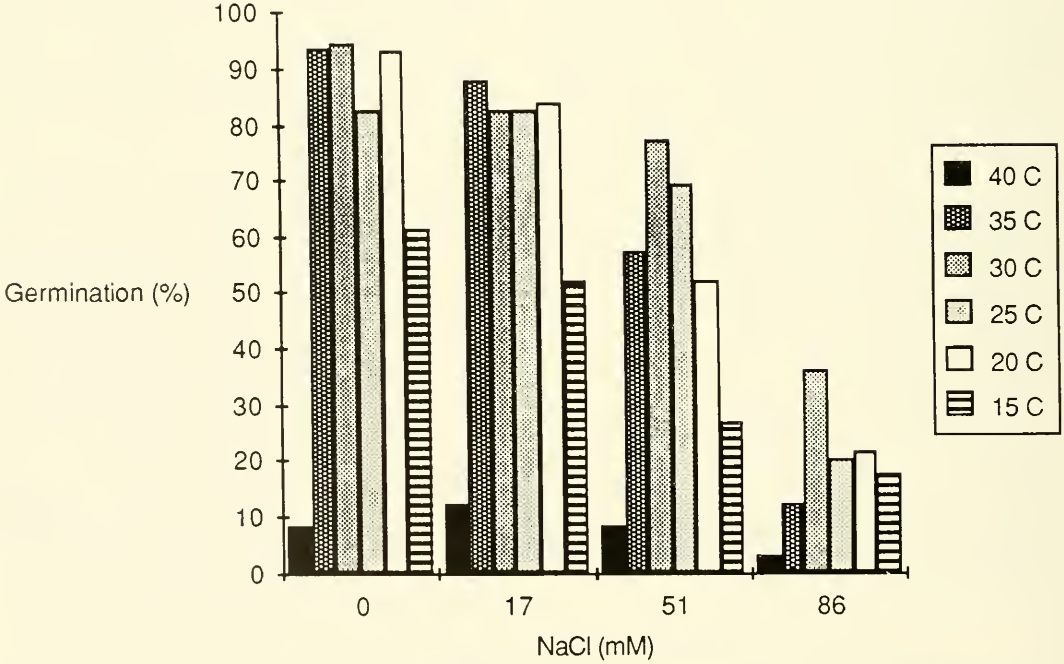

Fig. 2. Percent germination of seeds of *Chrysothamnus nauseosus* ssp. *viridulus* at constant temperatures and three concentrations of NaCl.

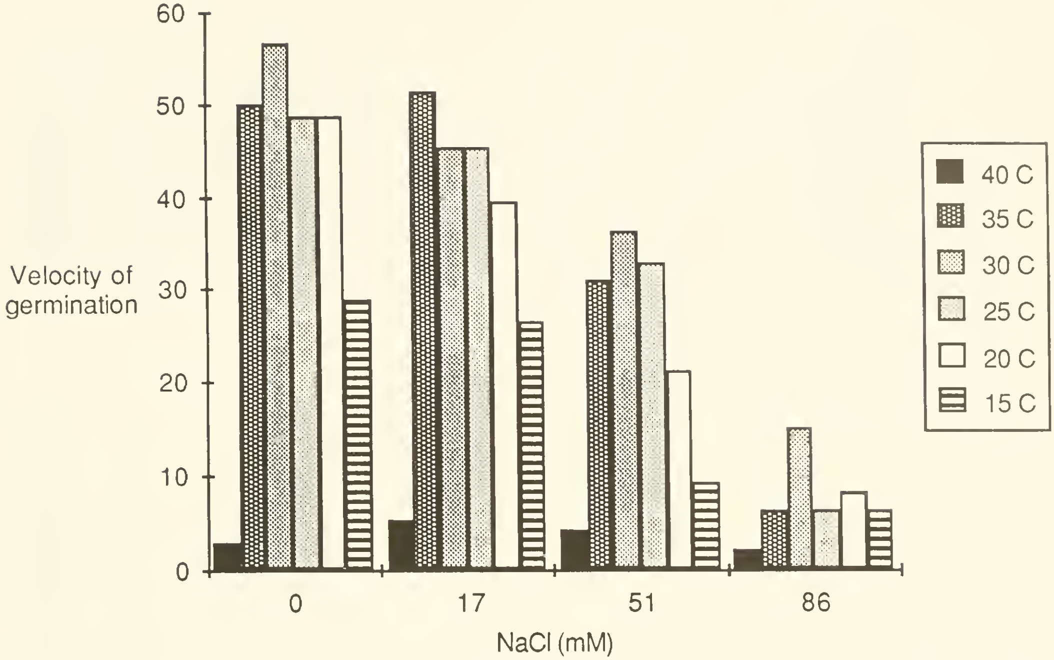

Fig. 3. Rate of germination (velocity of germination) of seeds of *Chrysothamnus nauseosus* ssp. *viridulus* at constant temperatures and three concentrations of NaCl.

germination velocity = G/t, where G = percentage of seed germinated at one-day intervals, t = total germination period (Khan and Ungar 1984).

Percentage germination data were transformed (Arcsin percent) before statistical analyses. The treatments were compared with Duncan's multiple range test.

RESULTS AND DISCUSSION

LIGHT AND TEMPERATURE EFFECTS.—Rabbitbrush seeds were germinated in light and dark conditions at constant and alternating temperatures. There were no differences in germination response between seeds germinated in light or in dark (Tables 1, 2), suggesting that the seeds were insensitive to light. Alternating temperature regimes of 20–30 and 15–25 C yielded maximum germination. Substantially less germination occurred in the 5–15 and 5–25 C temperature treatments (Tables 1, 2). Rate of germination estimated by using an index of germination velocity indicated that rates of germination at 15–25 and 20–30 C were twice as high as those of 5–15 and 5–25 C treatment (Fig. 1). These results indicate that low night temperatures inhibit both the rate and the final germination percentages. Sabo et al. (1979) reported that seeds of *C. nauseosus* ssp. *consimilis* germinated well with a peak percentage of 76% at alternating temperatures of 13–27.5 C. Alternating temperatures of 13–27.5 C (8 h) and 23–27.5 C (16 h) gave the best range responses, with germination times increasing slightly at the cooler temperature (Sabo et al. 1979).

Rabbitbrush seed germinated substantially at constant temperatures including 35 C (α = .05) (Fig. 2). Sabo et al. (1979) reported that germination of *C. nauseosus* ssp. *consimilis* was inhibited at a temperature above 27.5 C. The rate of germination of *C. nauseosus* ssp. *viridulus* was maximum at 30 C and decreased with either an increase or decrease in temperature (Fig. 3). At 40 and 15 C, the velocity of germination was significantly reduced.

SALINITY EFFECT.—NaCl salinity significantly inhibited (α = .05) the rabbitbrush seed germination at a concentration of 86 mM (Tables 1, 2). Rates of germination were significantly reduced (α = .05) at higher salinity (51 and 86 mM NaCl) (Table 1, Fig. 3). No interaction of light, temperature, and salinity was observed to affect seed germination. This spe-

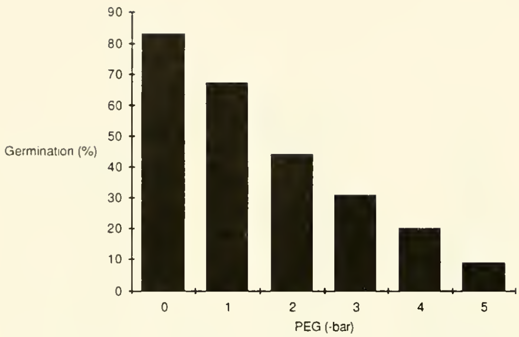

Fig. 4. Percent germination of seeds of *Chrysothamnus nauseosus* ssp. *viridulus* at different levels of moisture tension.

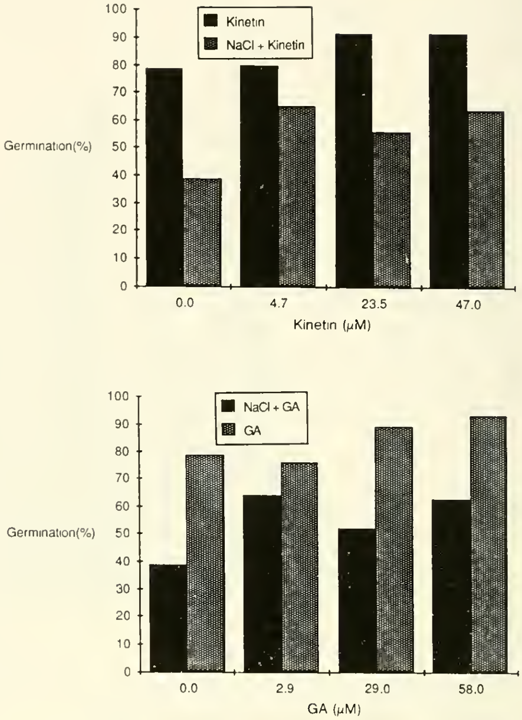

Fig. 5. Effect of kinetin and gibberellic acid on the germination of seeds of *Chrysothamnus nauseosus* ssp. *viridulus* in relation to three concentrations of NaCl.

cies has been reported to be highly salt tolerant (Sabo et al. 1979, Roundy et al. 1981), but our study indicated that it behaved like typical glycophytes at the germination stage. In natural field situations, seed germinates and seedlings could become established when precipitation dilutes natural high-salt concentrations. Once established, plants can tolerate relatively harsh conditions. In natural stands, *C. nauseosus* ssp. *viridulus* grows in alkaline valleys (Hall and Clements 1923).

Moisture Stress

Rabbitbrush seed germination was progressively reduced as the moisture tension increased to −5 bar (Fig. 4). At −5 bar treatment, less than 10% of seeds germinated compared to 85% in control. Seeds of *C. nauseosus* ssp. *consimilis* showed 34% germination at −7 bar treatment (Sabo et al. 1979).

Plant Growth Substances

Various concentrations of kinetin and GA_3 promoted germination of *C. nauseosus* ssp. *viridulus* as compared to nontreated control. NaCl (>51 mM) significantly ($\alpha = .05$) inhibited germination. This salt-induced inhibition was reduced by the inclusion of various concentrations of kinetin and GA_3 in the medium (Fig. 5).

Inhibition of seed germination induced by high salt concentration could be alleviated by application of GA_3 (Ungar and Binet 1975, Boucaud and Ungar 1976, Ungar 1977, Ungar 1984, Khan and Ungar 1985) and cytokinins (Boothby and Wright 1962, Odegbaro and Smith 1969, Kaufmann and Ross 1970, Ross and Hegarty 1980, Bozcuk 1981, Khan and Ungar 1985).

High salt concentrations induce dormancy in seeds of many plant species (Hydecker 1977). Boucaud and Ungar (1976) found that salinity depresses seed cytokinin levels but not the concentration of GA_3. However, dormancy induced by salinity, which may be similar to that caused by emergence-restricting seed coats, was broken by an application of GA_3 but not by kinetin (Ungar 1977). Khan and Ungar (1985) reported that GA_3 and kinetin can break salt-induced dormancy in *Atriplex triangularis*, suggesting that when exposed to salt stress, seeds of various species behave differently in response to exogenous application of growth substances.

Inhibition of germination caused by high temperature (40 C) can also be partially alleviated by addition of GA_3 and kinetin in the medium (Table 3). In addition, GA_3 and kinetin also partially alleviated the inhibitory effects of salt and higher temperature on germination.

TABLE 3. Velocity of germination and germination percentage at 40 C with NaCl, Ga_3, and kinetin.

Treatment	Velocity of germination	% germination
Control	15.0	27.9
NaCl (51 mM)	10.0	16.0
GA_3 (20 ppm)	21.7	43.9
Kinetins (10 ppm)	24.3	47.9
Salt + GA_3	19.0	36.0
Salt + kinetins	27.3	47.9

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DEVELOPMENT AND LONGEVITY OF EPHEMERAL AND PERENNIAL LEAVES ON *ARTEMISIA TRIDENTATA* NUTT. SSP. *WYOMINGENSIS*[1]

Richard F. Miller[2] and Leila M. Shultz[3]

ABSTRACT.—Big sagebrush (*Artemisia tridentata* Nutt.) is one of the most successful plants in the Great Basin based on its abundance and wide distribution. The development of dimorphic leaves may be an important mechanism attributing to its adaptive and competitive abilities. Development, persistence, and proportions of ephemeral and perennial leaves on Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis*) were studied for two years. The large ephemeral leaves are the first to develop in early spring. As early developing ephemerals mature and stems elongate, new ephemeral and perennial leaves develop in the axes of these large ephemerals. Perennial leaves expanded in the summer of their first growing season, persisting on the shrub until their abscission during summer drought of the second growing season. Plants maintained 33% of their leaf weight through the winters of 1985 and 1986. Active leaf and stem growth occurred at soil water potentials above −0.2 MPa.

During the past 100 years, big sagebrush (*Artemisia tridentata* Nutt.) has increased in abundance and distribution in many areas of the Great Basin. Success of this shrub throughout its range may be attributed in large part to the dimorphic development of ephemeral and perennial leaves. Caldwell (1979) suggests that the ability of the plant to maintain part of its leaf crop through the winter enables it to begin growth and utilization of water in early spring. Development and maintenance of large ephemeral leaves during optimum growing conditions may also increase photosynthetic potential by reducing mesophyll resistance (DePuit and Caldwell 1973).

Development and persistence of ephemeral and perennial leaves on big sagebrush growing in the Great Basin are poorly understood. Little work is available on timing and position of ephemeral leaf development in relation to perennial leaves. Confusion exists regarding the longevity of ephemeral and perennial leaves. On big sagebrush growing east of the Rocky Mountains, mature leaves remaining on the plant over winter are discarded soon after spring growth resumes (Diettert 1938, Branson et al. 1976). On three subspecies of big sagebrush growing in the Great Basin, Miller et al. (1986) reported overwintering leaves remained green on the plant through the subsequent growing season. These leaves senesced during initiation of summer drought, concurrent with abscission of the large ephemeral leaves. A clear picture of big sagebrush leaf development will enhance our understanding of why this plant is the most abundant and widespread shrub throughout the Great Basin. Objectives of this study were: (1) define the sequence and development of ephemeral and perennial leaves, (2) measure retention of the different leaf types, (3) define the proportion of both leaf types occurring on the plant, and (4) relate the developmental sequence to soil moisture.

MATERIALS AND METHODS

Research was conducted at the Squaw Butte Experimental Range in southeastern Oregon on the northern fringe of the Great Basin. The study site was located in a Wyoming big sagebrush–Thurber's needlegrass (*Artemisia tridentata* ssp. *wyomingensis* Nutt.–*Stipa thurberiana* Piper) habitat type. The 40-year mean annual precipitation is 300 mm. The study was conducted from September 1984 through August 1986.

In November of 1984 and 1985 three branches from each of five Wyoming big sagebrush plants were marked with metal tags. At the terminus of each branch all leaves were marked with a dot of black indelible ink, counted, and leaf length measured. On 1

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April 1984 and 1985, prior to leaf elongation, all marked leaves were counted and leaf length measured. Measurements on marked leaves were continued at two-week intervals throughout both growing seasons. Detailed notes and drawings were also made on current year's leaf and stem development.

Ten Wyoming big sagebrush plants were randomly selected for measurement of proportion of leaf types in 1985. These plants were harvested just past peak leaf development, when leaf growth and vegetative stem elongation had terminated and early signs of senescence were visible. Each plant was placed in a large plastic bag, brought into the lab, and leaves separated into four categories. The four leaf categories were 1984 perennial, 1985 perennial, lobed ephemeral, and nonlobed ephemeral occurring on reproductive stems. The 1984 and 1985 perennial leaves were easily differentiated by color, the current year's crop being lighter. Leaves were then dried for 48 hours at 60 C and weighed.

Soil water and soil temperature measurements were recorded concurrently with phenology. Soil water was measured gravimetrically at two depths, 2–20 cm and 20 cm to the hardpan, which varied from 40 to 50 cm. Soil moisture release curves for each of the two layers sampled were developed to convert percent soil water to soil water potential. Soil temperatures were measured with a soil thermometer at 15-cm and 30-cm depths.

Results

Big sagebrush is a semi-evergreen shrub, maintaining a portion of its leaves through the winter. All perennial leaves marked in the fall of 1984 and 1985 persisted through the winter, spring, and early summer, senescing at the onset of summer drought in late July of 1985 and 1986, respectively. Leaf longevity totaled 12 to 13 months, with no leaves persisting through two winters. Winter-persistent leaves, which only partially elongated during the previous growing season, did not reinitiate elongation the subsequent spring.

The large ephemeral leaves are the first to develop early in the spring from small leaf buds, less than 1 mm in length, at the stem apex. Leaf elongation begins in early spring forming tight clusters or fascicles at stem apices prior to stem elongation. When stems begin to elongate, ephemeral leaves are alternately positioned along the stem (Fig. 1). These early ephemeral leaves are the largest leaves on the plant. As spring progresses and the early ephemeral leaves near maturity (full leaf extension), a small cluster of leaves begins to develop in the axes of ephemeral leaves. These leaf fascicles contain both ephemeral and perennial leaves.

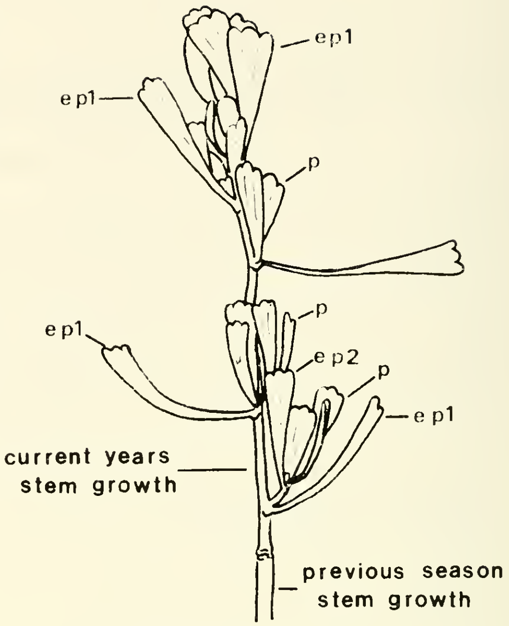

Fig. 1. Current year's growth near peak development with large early ephemeral leaves (ep1), later-developing ephemerals (ep2), and winter-persistent leaves (p). If stems do not elongate, separation of individual leaf clusters is more difficult to distinguish. Last year's winter-persistent leaves are not included.

Lateral leaf fascicles are properly termed "short shoots." Each short shoot fascicle is subtended by a long shoot and large eral leaf (Fig. 1). Later-developing ephemeral leaves are smaller than the early ephemerals but larger than the fully expanded perennial leaves. Not all fascicles contain this smaller ephemeral leaf, while some contain two. Ephemeral leaves on the reproductive stems are nonlobed and have no short shoot fascicles in their axes. At the onset of drought, both the previous season perennial and large, early-developing ephemeral leaves begin to senesce. Later-developing ephemerals, including nonlobed leaves, persist during the initial phase of leaf fall, senescing in late sum-

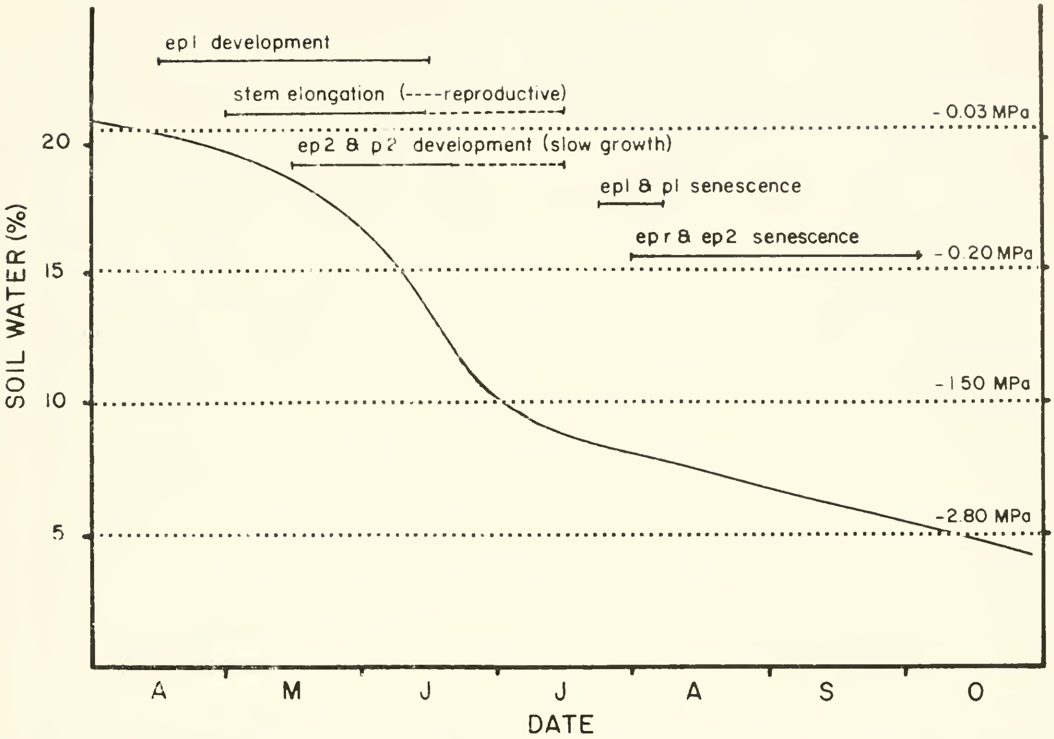

Fig. 2. Relationship of various stages of leaf development and senescence with soil water at 20 to 40+ cm; early ephemerals (ep1), ephemerals in axes of ep1 (ep2), previous year's perennials (p1), current year's perennials (p2), nonlobed ephemerals on reproductive stems (epr). Plant growth and soil water data derived from 1981, 1982, 1985, and 1986.

mer and fall. By November only the current crop of perennial leaves persists.

At initiation of plant growth, soil temperatures were 9 and 5 C at both 15- and 30-cm depths in 1985 and 1986, respectively. The majority of leaf and stem development occurred when soil water potentials were above −0.2 MPa in the wettest soil layer (Fig. 2). All the large ephemeral leaves were developed at this time. Once soil water potential in the wettest soil layer dropped below −0.2 MPa, elongation of primary vegetative stems terminated and leaf growth declined at a rapid rate. At soil water potentials between −0.2 MPa and −1.5 MPa, reproductive stems continued to elongate and short shoots elongated to a small degree. Limited growth of current year's perennial leaves continued, while previous season's winter-persistent leaves and the early large ephemerals began to senesce. All stem elongation and leaf growth terminated when soil water potentials dropped below −1.5 MPa. The majority of winter-persistent leaves of the previous growing season and early ephemerals senesced within a two-week period.

The relative proportion of perennial leaves remained nearly constant during the two growing seasons. At peak leaf development, leaf biomass on vegetative stems was 38 ± 4% previous season's perennial leaves (1984), 24 ± 3% ephemeral leaves, and 37 ± 3% current season's perennial leaves (1985) (at P = 0.90). Total leaf biomass consisted of 87 ± 6% lobed leaves and 13 ± 6% nonlobed leaves on the reproductive stems. Reproductive stem numbers were highly variable across the 10 shrubs, with nonlobed leaf biomass ranging from 2.5 to 28.5%.

DISCUSSION

Our observations of leaf development and longevity of Great Basin big sagebrush do not fully agree with those reported by Diettert (1938) and Branson et al. (1976). We conclude that the life span of winter-persistent leaves is approximately one year and that they persist through a second growing season, senescing at the onset of summer drought rather than at the beginning of the growing season. Branson et al. (1976) concluded that only 1 of 10 leaves marked on big sagebrush persisted on the plant (although this may be an artifact of marking leaves prior to or during the early stages of perennial leaf development). Their data indicate the plant maintains only 10% of its leaf numbers during the winter. On plants growing in the Great Basin, we found Wyoming big sagebrush retained 33% of its leaves, on a weight basis, throughout winters of 1985 and 1986. This compares more closely with Miller et al. (1986) where 53% of the leaf weight (lobed leaves only) senesced at the onset of summer drought. Had their data included nonlobed ephemerals on the reproductive stems, percent leaf weight lost may have approached 66%.

Early large ephemerals were first of the current year's leaf crop to abscise. Ephemeral leaves developed in the axes of the large ephemerals senesced throughout the summer and fall. This agrees with Diettert's (1938) observation that those leaves produced early in the year may be shed before the hot, dry periods of summer, although there is continuous but less conspicuous fall throughout the year.

The majority of plant growth, with the exclusion of reproductive stems, occurred at soil water potentials above -0.2MPa. This is consistent with plant growth and soil water data collected in 1981 and 1982 for three subspecies of big sagebrush (Miller et al. 1986). DePuit and Caldwell (1973) reported photosynthesis in big sagebrush is inhibited by moderate plant water stress.

Persistence of winter leaves allows evergreen plants an earlier start in utilizing nutrients and soil water than herbaceous or deciduous shrub species which have little or no leaf area displayed at the beginning of the growing season. Soil water is depleted more rapidly early in the growing season around isolated Wyoming big sagebrush plants than around isolated plants of green rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*), as well as in plots containing only perennial grasses (Eastern Oregon Agricultural Research Center data file). This is primarily due to a larger transpiration surface displayed early in the growing season. Success of big sagebrush may also be partially related to the display of numerous leaves during the cool season of the year prior to the development of moisture stress (Caldwell 1979). Leaf conductance of ephemeral leaves is higher than in persistent leaves (Eastern Oregon Agricultural Research Center data file), indicating photosynthesis per unit leaf area may be higher. The ratio of leaf surface to leaf weight is also higher for ephemerals than perennials (Ganskopp and Miller 1986), indicating the expense of resources used to develop the ephemeral leaf surface may be less than for persistent leaves. These large eral leaves enable the plant to effectively utilize resources during optimum growing conditions. When water becomes limiting, the plant responds by reducing its leaf surface area, abscising the large ephemeral and previous season persistent leaves.

ACKNOWLEDGMENTS

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PYGMY RABBITS IN THE COLORADO RIVER DRAINAGE

C. L. Pritchett[1], J. A. Nilsen[1], M. P. Coffeen[2], and H. D. Smith[1]

Abstract.—A range extension of the pygmy rabbit, *Brachylagus idahoensis*, into the Colorado River basin and a hypothesis as to its route of emigration.

The following report records the occurrence of *Brachylagus idahoensis* (Merriam) beyond its published range in the Bonneville Basin. The southeastern record of occurrence is 4.8 km NE Panguitch, Garfield Co. (Stephenson 1966). Holt (1975) reported "an isolated population about 15 miles south of Fish Lake on the Parker Mountain." On 7 July 1982 Michael Coffeen, Utah Division of Wildlife Resources, collected a pygmy rabbit ca 16 km S of the Fish Lake Ranger Station in Wayne Co., T28S R1E S14, elev. 2,379 m, and on 12 September 1982 Mark Oveson, unaware of Coffeen's specimen, reported seeing pygmy rabbits 4.8 km W of Loa, T28S R1E S3, elev. 2,183 m Wayne Co. (personal communication). Since then six live individuals plus two skulls have been collected from the Parker Mountain region of Awapa Plateau. The live animals were used for preparing karyotypes and saved as voucher specimens. This is the first published report of pygmy rabbits outside the Pleistocene Lake Bonneville (Columbia River) drainage. Awapa Plateau is part of the Fremont River watershed that eventually enters the Colorado River. Two of the specimens were females and two were males, but sex was not determined on the other three. Selected mean measurements (in millimeters) of two females and two males compared with means from *Brachylagus* reported by Janson (1946) in parentheses were as follows: Tot. L. 251, 218 (291) (278); Tail L. 20, 18 (17) (17); H.F. 66, 63 (70) (70); Ear. 52, 56 (50) (51). Means of greatest length of skull ($N = 8$) compared with means of the same measurement on skulls from 23 pygmy rabbits from Dubois, Idaho, are respectively 51.8 (S.E. = 0.72) to 49.8 (S.E. = 0.54). The voucher specimens and the comparison skulls of the Idaho rabbits were deposited in the mammal collection of the Life Science Museum, Brigham Young University. The rabbits and their sign (burrows and pellets) were essentially confined to tall big sagebrush, *Artemisia tridentata*, stands in shallow washes. This is consistent with other observations on pygmy rabbit habitat as reported by Merriam (1891), Grinnell et al. (1930), Orr (1940), and Green and Flinders (1980). According to some of the older ranchers in Loa, these "little rabbits" have been there as long as they can remember and have been extensively hunted along with cottontails and black-tailed jackrabbits (personal communication, 1984).

Assuming that big sagebrush is essential for these mammals, there are three possible routes of dispersal that might have been used by the pygmy rabbit to emigrate from the Great Basin to the Awapa Plateau (Fig 1). One route would be to exit the Great Basin and Sevier River by following the valley formed by Peterson Creek, near Sigurd, Sevier Co., up to Awapa Plateau. This is essentially the same route now used for Utah Highway 24. The other two routes leave the Great Basin from NE Iron Co. Janson's (1946) distribution map indicates a population of pygmy rabbits 24 km NW of Parowan, Iron Co. Individuals from this or nearby populations could have emigrated east through Buckskin Valley and Dog Valley into the Sevier River drainage SW of Circleville, Piute Co. From that point the most direct route would have been to follow the Sevier River down to its junction with East Fork of the Sevier River north of Circleville, thence east past Kingston along the

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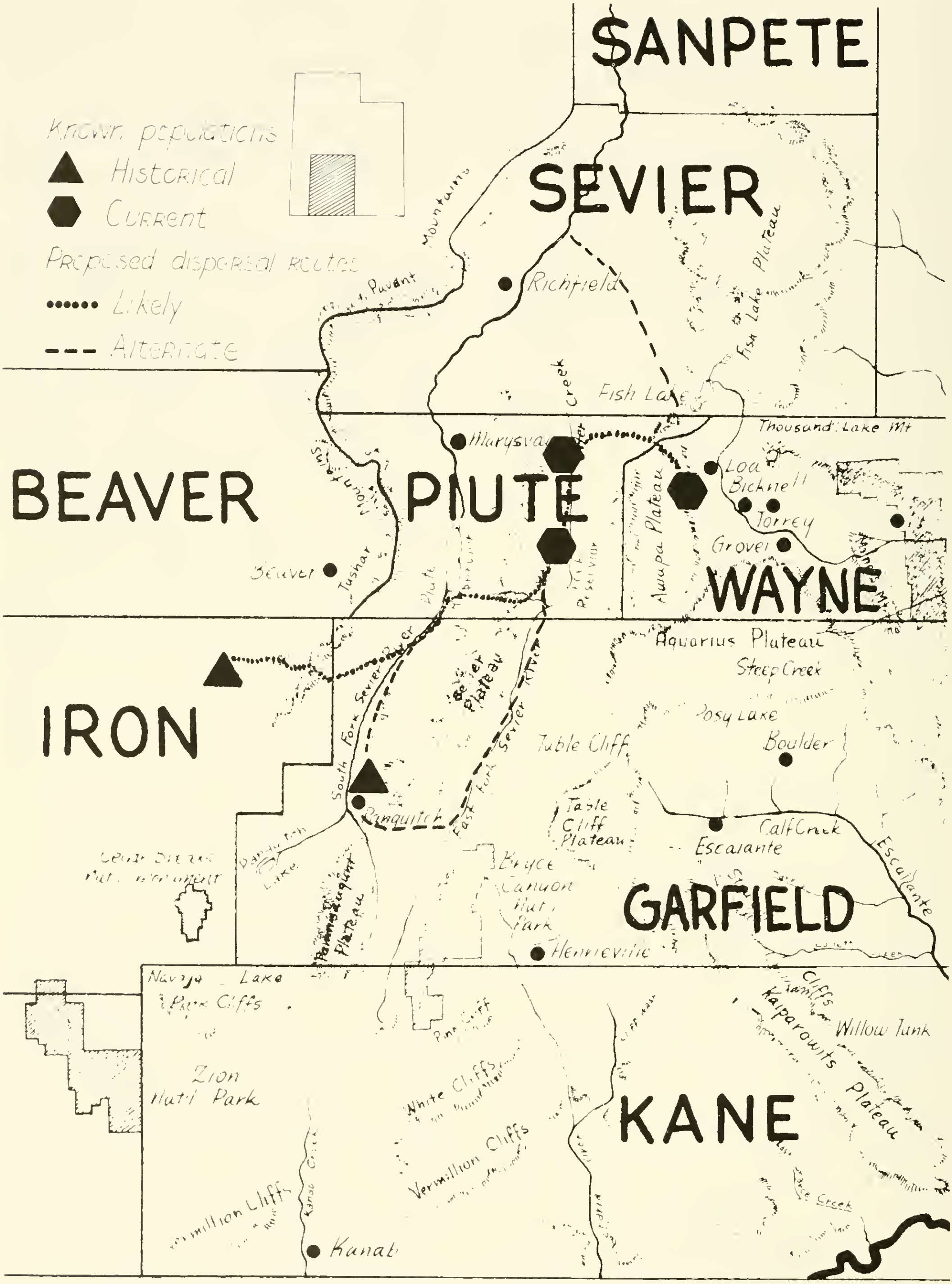
Known populations
Historical
Current
Proposed dispersal routes
Likely
Alternate
SANPETE
SEVIER
BEAVER
PIUTE
WAYNE
IRON
GARFIELD
KANE
Pavant Mountains
Richfield
Fish Lake
Fish Lake Plateau
Otter Creek
Marysvale
Thousand Lake Mt
Loa
Bicknell
Torrey
Grover
Awapa Plateau
Tushar Mountains
Beaver
Piute Reservoir
South Fork Sevier River
East Fork Sevier River
Sevier Plateau
Aquarius Plateau
Steep Creek
Posy Lake
Boulder
Table Cliff
Table Cliff Plateau
Escalante
Calf Creek
Panguitch
Panguitch Lake
Paunsaugunt Plateau
Cedar Breaks Nat. Monument
Bryce Canyon Nat'l Park
Henrieville
Navajo Lake
Pink Cliffs
Zion Nat'l Park
White Cliffs
Vermillion Cliffs
Kanab Creek
Kanab
Kaiparowits Plateau
Willow Tank
Escalante

Fig. 1. Locations of historic and present pygmy rabbit populations in the study area and routes of proposed emigration.

lower portion of East Fork of the Sevier River to Otter Creek. This route would then follow Otter Creek drainage north through Grass Valley to the Parker Mountain Range. Once into the Sevier River drainage near Circleville an alternate route might have followed the Sevier River south to Panguitch, the location of Stephensen's (1966) pygmy population, and on south along the river to its junction with Red Canyon. This route would then cross Paunsaugunt Plateau through Red Canyon and Coyote Hollow into Emery Valley, just north of Bryce Canyon National Park. The East Fork of the Sevier River flows through Emery Valley, a historic sagebrush community, to its junction with Otter Creek. From this junction pygmy rabbits could have followed the route previously suggested through Grass Valley to Parker Mountain.

During the summer of 1986, we spent several days following the proposed routes looking for pygmy rabbits and pygmy rabbit sign. Both their pellets (they pile their tiny, hard pellets like pack rats) and burrows (entrance shape) are distinctive. We were able to find pygmy rabbits or their sign from Burrville, ca .8 km northwest of Parker Mountain, south through Grass Valley to just north of Otter Creek Reservoir where big sagebrush ends and cultivated land and pastures begin. Holt (1975) found a small population of pygmy rabbits west of Otter Creek Reservoir. However, we were not able to find that population. The valley between Kingston and Otter Creek is narrow and very disturbed. One of the last large patches of big sagebrush along this 19-km route had just been plowed and harrowed which made it impossible for us to tell if pygmy rabbits were or had been there. We found no sign of pygmy rabbits from Sigurd to Burrville, and no pygmy rabbits or sign were observed through Emery Valley. Because of these observations, we feel the route from northeastern Iron Co. to the junction of the East Fork of Sevier River, up to Otter Creek and north through Grass Valley to Parker Mountain to be the most logical dispersal route for this group of lagomorphs.

We appreciate the comments and helpful suggestions made by Drs. W. Z. Lidicker, J. L. Patton, and David Ribble, all from the Museum of Vertebrate Zoology, University of California, Berkeley.

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EFFECTS OF LAND CLEARING ON BORDERING WINTER ANNUAL POPULATIONS IN THE MOHAVE DESERT

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and Katherine Bell Hunter[2]

ABSTRACT.—Construction of a 10-MWe solar thermal power plant in Daggett, California, involved clearing and leveling 53 ha of desert land. Transient offsite effects of this construction were apparent as a reduced density of annual plants within 100 m downwind of the edge of the cleared area. *Schismus arabicus* populations recovered within four years, but *Erodium cicutarium* populations did not. The effects appeared to be related more to an interaction of seed-dispersal mechanisms with the large, open space than to the obvious sand movement and deposition associated with the clearing operations.

The solar thermal power plant (Solar I) completed in 1983 at Daggett, California, is the first of a type which could eventually cover large areas of the southwestern United States. It consists of a field of mirrors (heliostats) that focus sunlight on a collector atop a tower, the heat being used to generate electricity. Such power plants, requiring neither transported fuels nor emission of fuel residues, obviate many of the environmental effects expected of nuclear and fossil-fueled plants. We studied the desert biota in the vicinity of Solar I in a search for potentially detrimental environmental effects. Winter annuals, which are ubiquitous around the site and whose growth is closely related to environmental conditions, were moderately affected during the construction phase.

Native Mohave Desert winter annuals produce impressive displays of wildflowers at five- to ten-year intervals (Went 1949). There are now a number of introduced Eurasian species present nearly every year in relatively high densities. These introduced species are the main subject of this paper.

STUDY SITE

Solar I was constructed on land adjacent to the Southern California Edison Coolwater power plant at Daggett, California. It lies at an elevation of 590 m, lat. 34°53′N and long. 116°47′W. Annual rainfall averaged 92 mm between 1951 and 1974 at the Daggett airport 2 km S of the site. Rainfall was divided evenly between winter storms and summer thundershowers (NOAA 1977). Daily average temperatures during the spring growing season were roughly 8 (minimum) and 24 C (maximum). Winter annuals germinated between December and March and died in late April or early May between 1978 and 1983.

The bed of the Mohave River forms the northern boundary of the Coolwater site. The river rarely flows, and wind has deposited sand from its bed on the site. Soils are therefore sands at the surface, but lenses of silt and hillocks of clay have been bared by human disturbance.

Perennial vegetation at the site was removed in 1953 in anticipation of farming operations. The land was never farmed, however, due to a shortage of water (Robert Speth, personal communication). A population of the shrub *Atriplex polycarpa* dominated the site prior to the start of construction.

TABLE 1. Changes in heights of sand mounds on the lee sides of shrubs.

Distance from perimeter fence	10/78–1/80	1/80–5/81	5/81–10/81
meters	cm	cm	cm
26–37	18 ± 7*	10 ± 2	7 ± 2
40–49	14 ± 2	1 ± 1	0 ± 2
51–58	7 ± 2	2 ± 2	2 ± 2
60–79	—	—	3 ± 1
87–98	0.4 ± 0.2	1.1 ± 0.4	0.2 ± 0.2

*Error estimates are ± sem.

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TABLE 2. Wind ablation or dune growth as measured by changes in surface level downwind of the heliostat field during spring 1982.

Date	Distance from perimeter fence (m)			
	40 m mm	80 m mm	130 m mm	200 m mm
22 Feb–23 Apr	−3.3	−3.4	0	0.3
23 Apr–16 Jun	−1.8	+1.4	−1.1	0.7
16 Jun–10 Jul	+2.2	+1.1	+3.9	+1.4
22 Feb–10 Jul	−2.9 ± 1.4*	−0.9 ± 1.3	+2.8 ± 1.1	+0.4 ± 0.7

*Error estimates are ± sem

TABLE 3. Densities and sizes of *Schismus arabicus* and *Erodium cicutarium* plants with respect to distance from the heliostat field. Negative distances are on the field.

	Schismus			*Erodium*	
			1981		
Distance	n/m²	mg/plant		n/m²	mg/plant
0–100 m	280 ± 73*	2 ± 1		8 ± 4	9 ± 4
100–200 m	218 ± 70	9 ± 4		116 ± 4	77 ± 20
			1982		
40 m	400 ± 50	30 ± 4		0	—
80 m	1600 ± 250	14 ± 2		10 ± 4	112 ± 41
200 m	2100 ± 250	25 ± 3		24 ± 6	97 ± 24
			1983		
−100 m	17 ± 9	28 ± 10		0	—
−20 m	18 ± 10	150 ± 139		0	—
40 m	4800 ± 1800	28 ± 5		0	—
200 m	3100 ± 640	38 ± 11		80 ± 33	464 ± 202

*Error estimates are ± sem.

METHODS

Annual populations were measured in quadrats placed randomly along lines at specific distances from the perimeter fence surrounding the heliostat field. Initial studies were done with nested quadrats varying from 0.01 to 100 m² in area. Based on those studies, we chose quadrat sizes of 0.01 and 0.025 m² for these studies on the more abundant annuals.

All annual plants within a quadrat were counted, harvested, dried, and weighed. Because plants were harvested without loosening the soil, only small portions of the root systems were included.

Sand mounds deposited beneath and in the lee of shrubs were delimited by the presence of small pebbles on the original surface. Heights were measured from the highest point on the mound to the level of the nearest bare spot. In the spring of 1982, deposition-ablation of sand was determined by driving marked aluminum stakes into the ground and measuring changes in the apparent surface level with time.

Seeds dispersed near the boundary of the heliostat field were trapped on plastic 10-cm square plates coated on the top side with a tacky material (Tangletrap; The Tanglefoot Company, Grand Rapids, Michigan) and left at the ground surface from 26 April to 5 May 1983. Trapped seeds were counted using a dissecting microscope.

RESULTS

Native annual species, which were abundant in 1978 and present in 1979, did not germinate in significant numbers after clearing began in September 1979. Species that germinated and grew from 1980 to 1983 were the introduced annuals *Schismus arabicus* Nees, *Erodium cicutarium* (L.) L'Her., and *Salsola paulsenii* Litv. The latter was sparse.

Sand was deposited downwind of the heliostat field during and following clearing. Sand mound heights behind shrubs increased dramatically through 1981 in the area immediately adjacent to the cleared site (Table 1). In 1982, however, following installation of he-

TABLE 4. Effects of mounds and distance from the perimeter fence on density, size, and productivity of *Schismus arabicus* in 1982.

	Distance from fence (m)					
	40		80		200	
	Bare	Mound	Bare	Mound	Bare	Mound
Density (#/m^2)	4 ± 1*	3 ± 2	16 ± 5	9 ± 5	21 ± 5	11 ± 5
Size (mg/plant)	30 ± 8	61 ± 14	14 ± 4	43 ± 24	25 ± 6	75 ± 60
Biomass (kg/ha)	85 ± 32	141 ± 71	172 ± 46	124 ± 56	336 ± 82	313 ± 140

*Error estimates are 95% confidence limits.

TABLE 5. Densities of *Schismus arabicus* trapped seeds and floret parts in relation to the heliostat field edge. Negative distances are on the field.

Distance from fence (m)	Total seed #/cm^2	Chaff #/cm^2	Naked seed %
−100	0.4 ± 0.0*	5.3 ± 0.1	16 ± 4
−20	0.8 ± 0.0	4.8 ± 0.2	24 ± 3
40	3.6 ± 0.1	4.3 ± 0.1	3 ± 2
200	4.4 ± 0.2	1.3 ± 0.1	1 ± 0

*Error estimates are ± sem.

liostats, sand mounds were ablated in the first 50 m and deposition occurred further downwind. During the spring of 1982, marked aluminum stakes showed a similar pattern, with slight ablation occurring at sites 40 m from the heliostat field, slight deposition at 130 m, and no significant changes at 80 and 200 m (Table 2).

In 1981, a very poor year for growth and reproduction of annuals, the average size and density of *Erodium cicutarium* were reduced within 100 m of the eastern border of the heliostat field. Neither density nor size of *Schismus arabicus* differed with respect to distance from the border (Table 3). In 1982 *Schismus* densities were considerably reduced and *Erodium* was absent. Sizes of *Schismus* plants were reduced at 80 m, but *Erodium* size was the same at 80 and 200 m. In 1983 densities of *Schismus* had fully recovered 40 m from the heliostat field, sizes were constant at all distances, and *Erodium* was still absent (Table 3).

Comparison of populations on and off the sand mounds in 1982 showed the density depression at 40 m was not solely related to sand movement and drifting: densities were reduced both on the mounds and the bare areas. Sizes of *Schismus* plants were uniformly greater on the mounds than in the bare areas (Table 4).

Allocation of biomass to reproductive structures did not vary with location of plants. On the mounds the larger plants (69 ± 14 vs. 31 ± 9 mg/plant) contained 26 ± 2% biomass in reproductive structures, compared to 25 ± 3% for bare area specimens. These data, combined with the density differences between mound and bare populations (Table 4), imply that seed production was not depleted in the area of sand deposition.

Schismus seeds deposited in 1983 on and downwind of the heliostat field were not proportional to densities of plants (Table 5). Seeds deposited on the largely unvegetated field were considerably more dense than would be expected from the associated plant densities. In addition, the nature of the dispersal units found on the heliostat field suggested that seeds had traveled a greater distance. Seeds frequently lacked the pilose floral parts, and these parts, less seeds, were also more common (Table 5). *Erodium* seed was deposited only on traps 200 m from the perimeter fence, where a population occurred near the traps.

Seeds of other species were sparse on our traps. Seeds with pappuses (of several species) averaged 26 per 100-cm^2 plate on the heliostat field and 2 per plate in the control area. Seeds without any obvious adaptations for wind dispersal averaged 2 per plate on the heliostat field and 35 per plate in the control area.

DISCUSSION

Plant size was only transiently affected during clearing and construction of the heliostat field. This argues against changes in general environmental variables (light, wind speed, precipitation). The primary effects seen were on density, and the observations to be explained are the reductions in density and rates of population recovery. Because the effects were unexpected and transient, these explanations necessarily derive from observations after the fact.

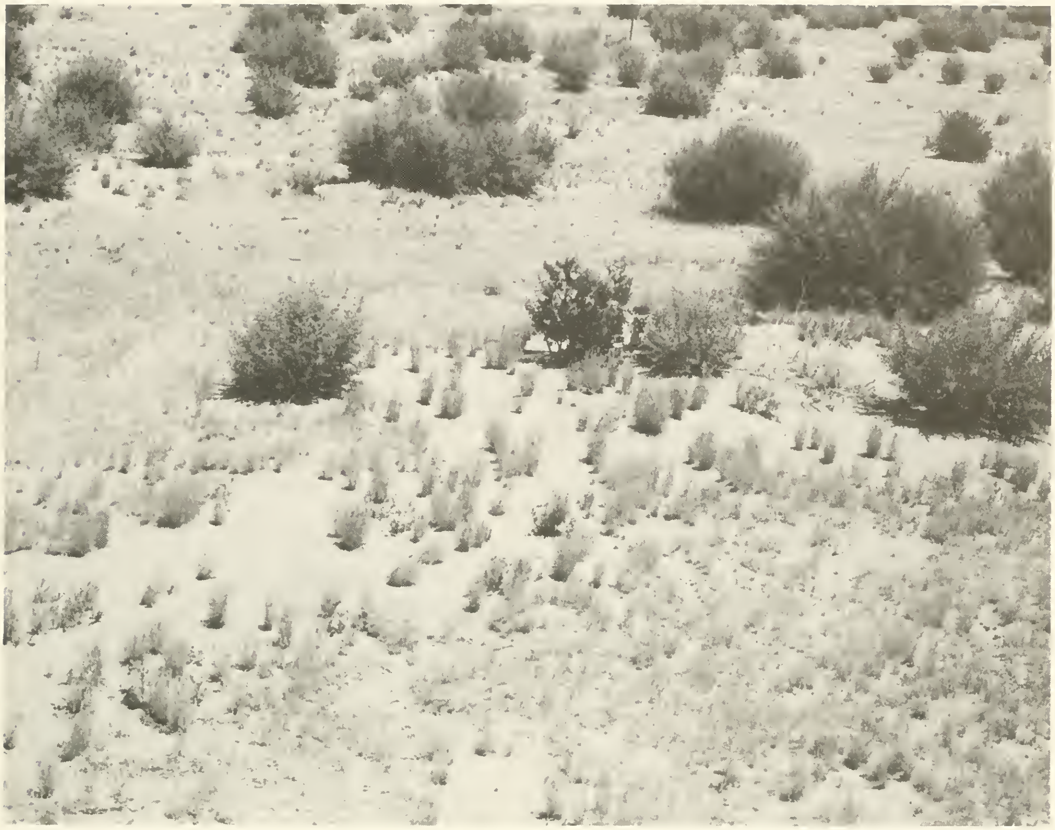

Fig 1. Plant populations on sand mounds downwind of the cleared heliostat field, April 1980. Shrubs are *Atriplex polycarpa* and the grass is *Schismus arabicus*.

Schismus density was reduced with respect to control areas only in 1982 (Table 4). During the 1981 harvest few *Schismus* in Daggett had flowers or fruit. We found 98% prereproductive mortality in another Mohave Desert *Schismus* population that year (unpublished data). Hence, we may presume 1982 populations were derived primarily from seeds produced in 1980 and earlier. Photographic evidence from 1980 (Fig. 1) suggests burial by sand affected density of *Schismus* on mounds, but increased plant size may have compensated and resulted in near normal seed production (Table 4, Fig. 1).

Seed burial by sand is not a satisfactory explanation for the reduced 1982 densities, since the density reduction occurred both on and off the sand mounds (Table 4). Invocation of Occam's razor suggests we look for an alternative hypothesis.

Another potential mechanism for low plant density was net immigration. Data in Tables 3 and 5 suggest that the large majority of seeds deposited on the heliostat field came from off the field. Seeds trapped per mg of plant were 3 to 8 on the heliostat field, 0.37 in the control area, and only 0.26 40 m east of the fence. Furthermore, the "chaff" (Table 5) can be considered an indicator of seeds moving onto the heliostat field. The proportions of chaff and naked seed found strongly suggest that *Schismus* dispersed greater distances near the heliostat field (40 m east) than in the control area (200 m east). There is, therefore, evidence that the large open field could act as a seed sink and that sand deposition was not a sufficient explanation for reduced densities. For *Schismus*, the rapidity of population recovery can be reasonably explained by the obviously effective dispersal demonstrated in 1983 (Table 5) coupled with good seed production in 1982.

Erodium cicutarium behaved somewhat differently. It became locally extinct near the heliostat field by 1982 and did not recover in 1983 (Table 3). We have fewer data on *Erodium* than on *Schismus*. In 1980, at 100–200 m from the heliostat field, essentially all *Erodium* fruited, while in 1981 roughly half had flowers or fruit at harvest (data not presented). In addition, in 1981 insects cut off many *Erodium* tap roots just below ground level, and ant mounds were seen with many *Erodium* seeds surrounding the holes. The local extinction, therefore, may be an interaction of several biotic and abiotic factors.

Failure of *Erodium* populations to recover could be related to both the causes of the original reduction and the failure of seed dispersal from the remaining inhabited sites. The failure to disperse might well be related to the *Schismus* population, since a dense *Schismus* stubble generally persists throughout the year.

Weiner and Conte (1981) modeled annual plant population dynamics and found dispersal "extremely important" in colonizing open areas. As disturbance becomes more frequent in the desert, we may well unwittingly favor weedy species with good dispersing abilities (like *Schismus* and *Salsola*) at the expense of the natives, which are unusually lacking in obvious dispersal mechanisms (Ellner and Shmida 1981).

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OCCURRENCE OF THE MUSK OX, *SYMBOS CAVIFRONS*, FROM SOUTHEASTERN IDAHO AND COMMENTS ON THE GENUS *BOOTHERIUM*

Michael E. Nelson[1] and James H. Madsen, Jr.[2]

ABSTRACT.—A set of ovibovine horn cores collected from Pleistocene sediments in southeastern Idaho provides additional evidence for sexual dimorphism in the helmeted musk ox, *Symbos cavifrons*. Specimens previously assigned to *Bootherium sargenti* are placed in synonomy with *Symbos cavifrons* as sexual dimorphs (females). *Bootherium bombifrons* is a valid taxon and is probably not closely related to *Symbos*.

The taxonomic status of the extinct musk ox, *Bootherium*, has been questioned since Leidy (1852a, 1852b) proposed the name for two extinct species of ovibovines, *B. bombifrons (Bos bombifrons* of Harland 1825, Wistar 1818) and *B. cavifrons*. Later, Dawkins (1867) and then Leidy (1869) synonymized these extinct forms with the extant musk ox, *Ovibos*. Osgood (1905a) erected the genus *Scaphoceros* for a musk ox, *S. tyrrelli*, collected from the Yukon Territory of Canada but later discovered that *Scaphoceros* was preoccupied; he therefore replaced it with the name *Symbos* (1905b). In addition, Osgood (1905a, 1905b) observed that *Symbos cavifrons* and *Bootherium bombifrons* were distinct species and definitely separable from the extant *Ovibos moschatus*. Gidley (1908) named a second species of *Bootherium*, *B. sargenti*, from a late-Pleistocene deposit in Michigan.

Taxonomists (see Kurten and Anderson 1980) now generally agree that all extant musk ox belong to *Ovibos moschatus* and that the various proposed species of *Symbos*, e.g., *S. tyrrelli* Osgood, *S. australis* Brown, *Liops zuniensis* Gidley (preoccupied, changed to *Lissops zuniensis* Gidley), and *Gidleya zuniensis* (Cossman) are all assignable to *Symbos cavifrons* (for a different opinion see McDonald 1985). However, the taxonomic status of *Bootherium* has remained in question.

Confusion surrounding *Bootherium* has arisen from the supposed sex of various *Bootherium* and *Symbos* skulls. Is *Bootherium* a female *Symbos*? Rutimeyer (1867), on the basis of Leidy's (1852a, 1852b) figures and descriptions, pronounced that *Bootherium cavifrons* (= *Symbos cavifrons*) was a male and *B. bombifrons* a female. He then assigned these specimens to a new taxon, *Ovibos priscus*. Dawkins (1872) came to a similar conclusion but chose to call the duo *Ovibos cavifrons*. Lydekker (1885, 1898) was also convinced that *B. bombifrons* and *B. cavifrons* (= *S. cavifrons*) were sexual dimorphic forms of the same species.

Osgood (1905a), as Allen (1913) so aptly stated,

> set forth the real facts of the case. . . . [S]ince *bombifrons* and *cavifrons* have been considered by several authors as being not only congeneric, but conspecific, the establishment of a separate genus for each may appear surprising. While it may be possible, from an examination of the figures only, to construct a hypothesis to the effect that *cavifrons* represents the male and *bombifrons* the female of one species, it is inconceivable that any modern taxonomist would reach such a conclusion after comparing the original types.

Allen (1913) certainly agreed when he stated,

> Upon carefully reading Osgood's paper I felt sure that he had correctly solved the problem.

Evidently Hay (1924) did not believe the problem had been solved and did "not accept this opinion [of Allen and Osgood]." Hay believed that some of the 25 skulls of *Symbos cavifrons* that he examined "must have been females."

Bison appalachicolus, originally named by Rhoads (1895), was assigned to *Bootherium appalachicolus* by Ray (1966a) and described as "closely related, if not conspecific" with *Bootherium sargenti*. *Bootherium nivicolens* was erected by Hay (1915) for a specimen from

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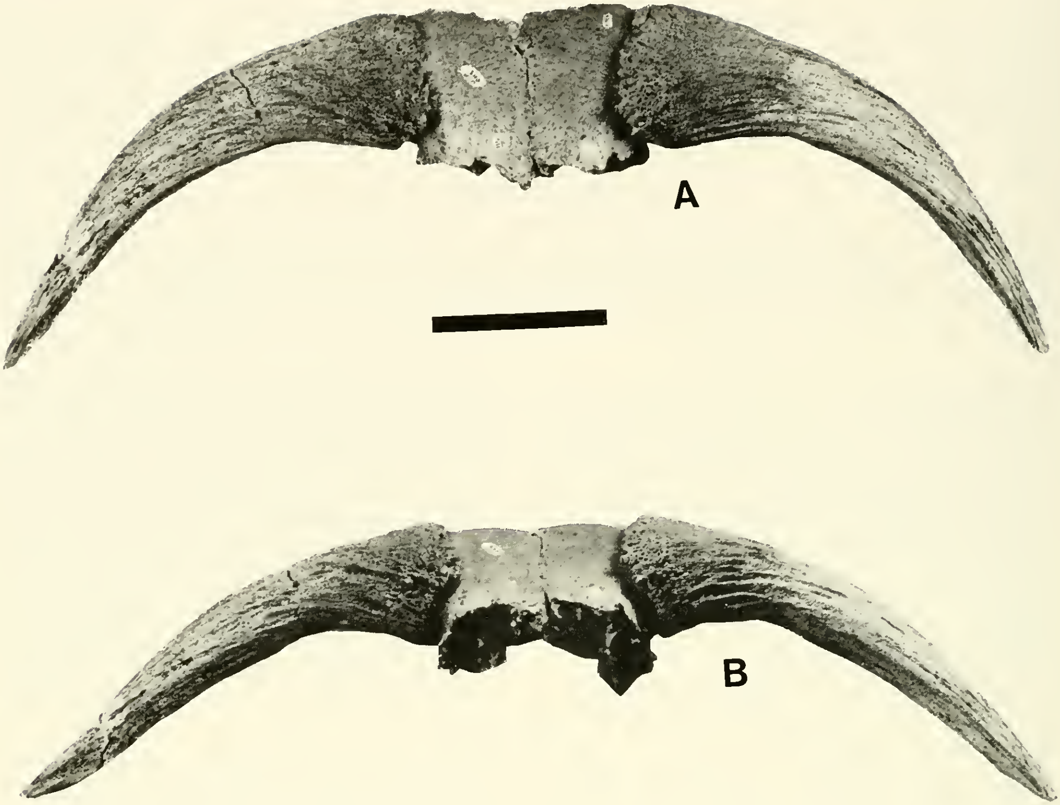

Fig. 1. *Symbos cavifrons*, UVP 083; A, Dorsal view of horn cores. B, Posterodorsal view. Bar represents 10 cm.

Eschscholtz Bay, Alaska, while Hesse (1942) named *Bootherium brazosis* from Brazos County, Texas. The latter has been identified by Ray (1966b) as conspecific with *Bootherium sargenti*.

Hibbard and Hinds (1960) reported,

> It is very likely that *Bootherium* is the female woodland musk ox since all specimens of *Symbos* based on skulls are considered those of bulls.

Evidently Hibbard and Hinds examined the type of *B. sargenti* and made their decision on the basis of this specimen. It is not known if they intended to also include *B. bombifrons* as a female *Symbos*.

Semken et al. (1964) reviewed the literature and decided

> that *Bootherium bombifrons* represents a genus distinct from *Symbos*. However, *B. sargenti*, the specimen examined by Hibbard and Hinds (1960), may be a female *Symbos*.

Ray et al. (1967) excavated an ovibovine cranium from Saltville, Virginia, that was assigned to *Bootherium* sp. indet., and stated that

> the specific taxonomy (not to mention the generic status) of *Bootherium* is not yet well understood.

Nelson and Madsen (1978) documented the existence of 21 individual musk ox from late-Pleistocene sediments of Utah. They assigned the four specimens of *Bootherium* to *Bootherium* sp. indet., although Stokes and Hansen (1937) had previously assigned one specimen (BYUG 834) to *B. bombifrons*.

Harington (written communication 1978) synonymized *Bootherium nivicolens* with *B. sargenti*. He also believed that *B. sargenti* was probably the female of *Symbos cavifrons* because the differences between the specimens parallel the morphological differences between male and female specimens of *Ovibos moschatus*.

In Kurten and Anderson's (1980) summarization of Pleistocene mammals of North America, *Bootherium sargenti* and *Symbos cavifrons* were synonymized, while the type specimen of *B. bombifrons* was questionably left as a separate species.

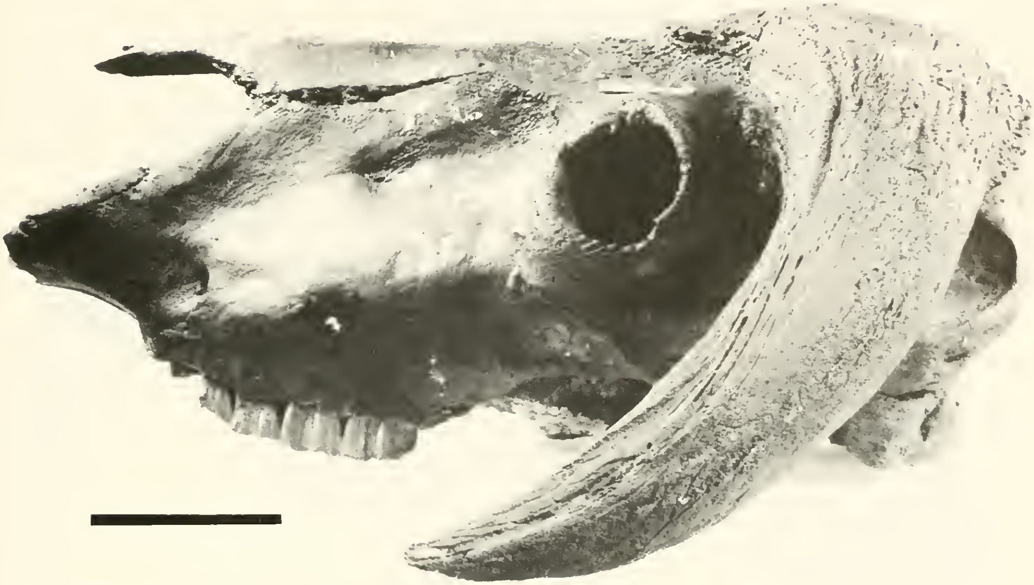

Fig. 2. *Symbos cavifrons*, UUVP 8540, left lateral view. Bar represents 10 cm.

White (personal communication 1984, 1985) reviewed the musk ox of Idaho and concluded that two cranial fragments of *Bootherium* collected from Pleistocene sediments in Idaho (IMNH 68001; LACM 6671) could not be assigned with confidence to established species. However, the size of the cranial fragment (LACM 6671) collected from Minidoka Dam "suggests it may be referable to *B. sargenti.*"

J. N. McDonald (Radford University) is studying a mummified specimen of *Bootherium* collected from a permafrost locality at Fairbanks Creek, Alaska (F:AM A-293–5286). Other than a preliminary report (McDonald 1984), little has been published on this interesting specimen.

Institutional abbreviations are as follows:

UVP-	Utah Division of State History, Antiquities Section, Vertebrate Collection
UUVP-	University of Utah, Vertebrate Paleontology Collection
IMNH-	Idaho Museum of Natural History
KUVP-	Kansas University, Vertebrate Paleontology
LACM-	Los Angeles County Museum of Natural History
GRPM-	Grand Rapids Public Museum
ANSP-	Academy of Natural Sciences of Philadelphia
TAMC-	Texas A & M University Collection
BYUVP,	BYUG-Brigham Young University, Vertebrate Paleontology Collection
USU-	Utah State University, Geology Collection
USNM-	United States National Museum of Natural History
F:AM-	Frick Collection, American Museum of Natural History

COLLECTION BACKGROUND

In 1980 Chris and Jack Dukes of Salt Lake City, Utah, brought a partial cranium with a complete, although broken, set of horn cores to the Antiquities Section of the Utah Division of State History. A laboratory assistant labeled the specimen "Bison, collected from Idaho" and entered the specimens into the collections. In examining these collections during the winter of 1985, we recognized the horn cores as ovibovine and not bison. The horn cores resembled the numerous horn cores of *Symbos cavifrons* in the Division of State History and Utah Museum of Natural History collections, but the frontal area of the cranium lacked the characteristic exostosis and median cranial sulcus of *Symbos*. Comparisons with Utah specimens of *Bootherium* revealed no close resemblances. This discovery prompted a review of all Utah and Idaho musk ox specimens and ultimately led to the preparation of this report.

AGE AND STRATIGRAPHY

Precise locality information and stratigraphic data were garnered after the discov-

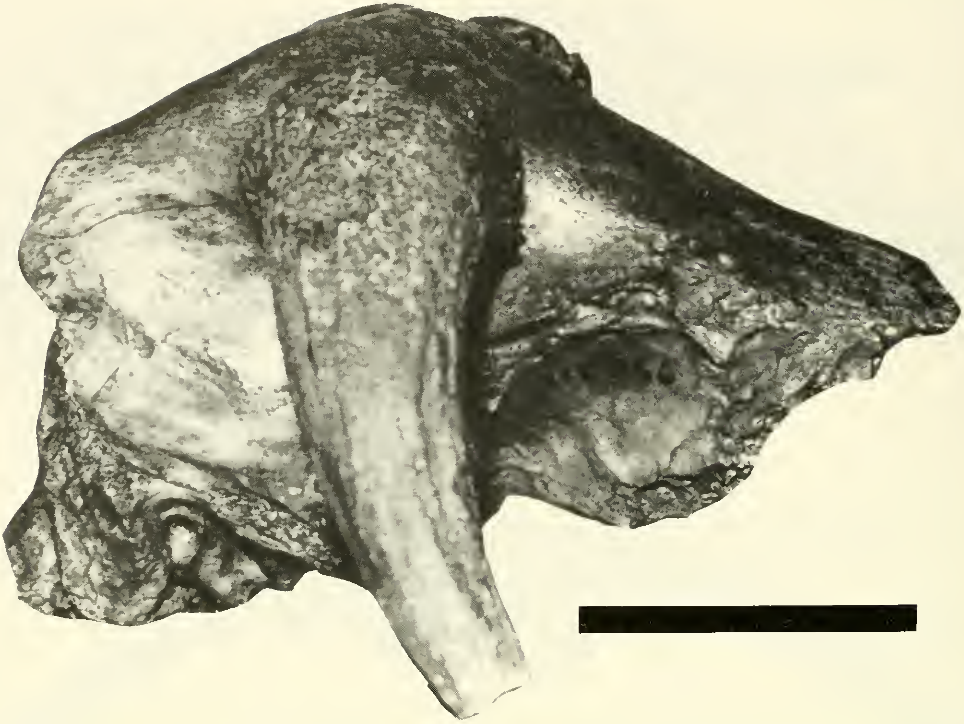

Fig. 3. *Bootherium bombifrons*, USNM 215066 (cast), original ANSP 2994, right lateral view. Bar represents 10 cm.

erer of record, Jerry Davis of Soda Springs, Idaho, was located. Davis collected the specimen 3 March 1977 during the excavation of a grain elevator shaft in American Falls, Idaho. This elevator, located at the intersection of Oregon Trail and Elevator Streets in American Falls, has the following legal description: NE1/4, Sec 29, T7S, R31E, Power County, Idaho.

The Dam local fauna (IMNH locality 52002), described from a gravel quarry located between the present American Falls townsite and the east end of the American Falls Dam (Hay 1927, Gazin 1935, Hopkins 1951, 1955, Hopkins, Bonnichsen, and Fortsch 1969, Barton 1976, White 1985), was collected approximately 200 m southwest of the elevator construction site. Among other fossils collected by Gazin (1935), White (1985) listed a number of specimens of *Symbos cavifrons* obtained from a pit in the American Falls Formation. A radiocarbon date on in situ bone fragments from the locality yielded a date of 26,500 ± 3,500 y.b.p. (Barton 1976). White (1985) believed the Dam l.f. was correlative with the "B layer" of Hopkins, Bonnichsen, and Fortsch (1969) and the Rainbow Beach section of McDonald and Anderson (1975).

Field relationships indicate that the new musk ox specimen (UVP 083) was collected from the same sediments as the Dam l.f. and is therefore a part of the Dam l.f.

SYSTEMATIC PALEONTOLOGY

Order Artiodactyla

Family Bovidae

Genus *Symbos* Osgood 1915

Symbos cavifrons (Leidy) 1852

Bootherium bombifrons Leidy 1852 (in part)
Ovibos cavifrons Dawkins 1883, Leidy 1869, Lydekker 1885, McGee 1887 (in part)
Bison appalachicolus Rhoads 1895
Ovibos cavifrons Hatcher 1902
Scaphoceros tyrrelli Osgood 1905
Symbos tyrrelli Osgood 1905 (*Scaphoceros* preoccupied)
Gidleya zuniensis Cossmann 1907
Lissops zuniensis Gidley 1908 (*Liops* preoccupied)
Symbos australis Brown 1908
Bootherium sargenti Gidley 1908
Ovibos appalachicolus Staudinger 1908, Allen 1913, Hay 1923, Frick 1937, Kitts 1953
Bootherium nivicolens Hay 1915
Symbos promptus Hay 1920
Symbos convexifrons Barbour 1934
Ovibos giganteus Frick 1937

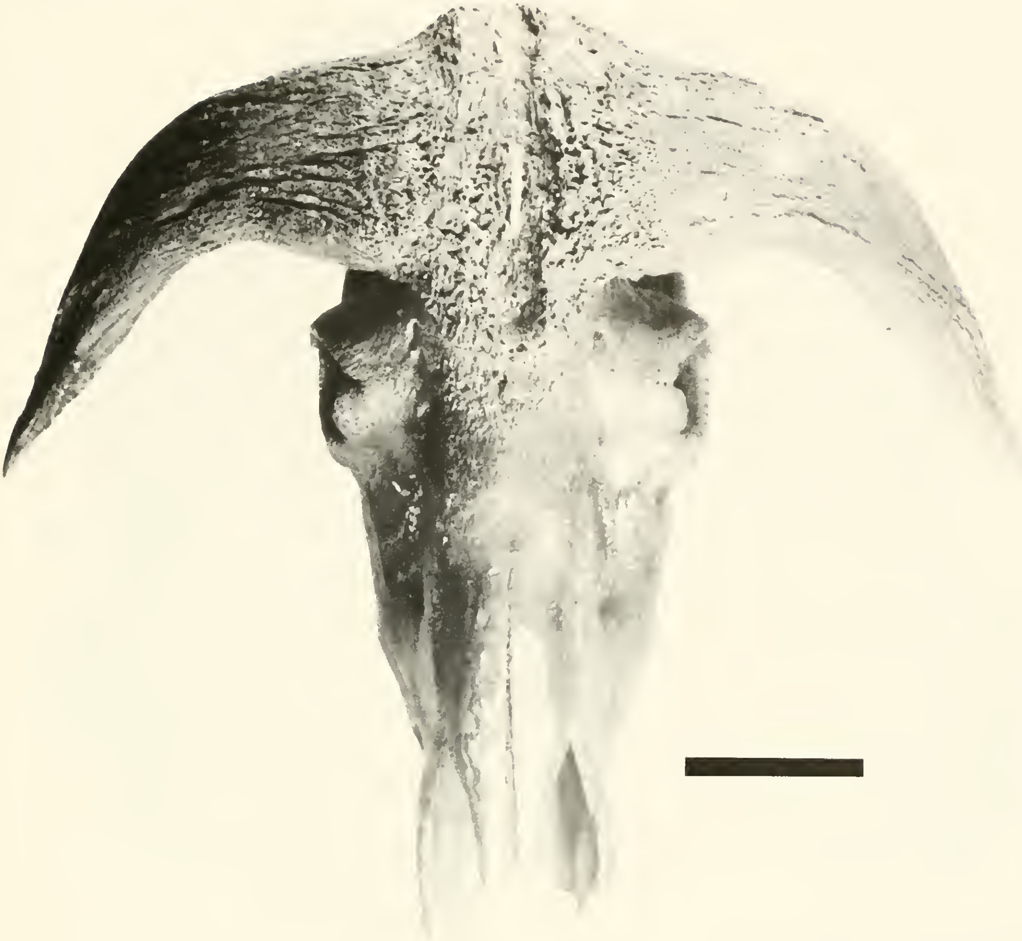

Fig. 4. *Symbos cavifrons*, UUVP 8540, dorsal view. Bar represents 10 cm.

Bootherium brazosis Hesse 1942
Bootherium appalachicolus Ray 1966
Bootherium sp. indet. Nelson and Madsen 1978 (in part)
Bootherium sp. White 1985 (in part)

MATERIAL.—UVP 083, cranial cap including both horn cores.

DESCRIPTION.—UVP 083 consists of a complete set of horn cores attached to the frontals and the cranial cap (Fig. 1). Very little of the cranium is preserved anterior or posterior to the attachment of the horn cores. The horn cores curve outward, downward, and forward with a high lateral flare and are very similar to the curvature on *Symbos* skulls that are thought to be males. However, the horn core tips of male *Symbos* skulls drop to a position that nears the base of the skull (Fig. 2). The horn cores on UVP 083 tend to flare out in a lateral direction and do not extend much below the orbits. This curvature contrasts with the horn core curvature seen in *Bootherium bombifrons*, where the horns flare only slightly outward and then drop sharply downward and finally forward (Fig. 3).

The horn cores in UVP 083 slightly overlap the frontals as on male *Symbos* skulls (Fig. 4). However, there is an absence of an exostosis and cranial sulcus, and the area on the frontals and parietals between the proximal borders of the horn cores is smooth (Fig. 1). A slightly elevated anterior-posterior ridge extends along the midline of the frontals.

A burr is neither present on the horn cores nor do the horn cores stand out on pedicles as in *Bootherium*. The horn cores are flattened on the dorsal surface near the proximal border. This condition is reflected in male *Symbos* horn cores and stands in contrast with the

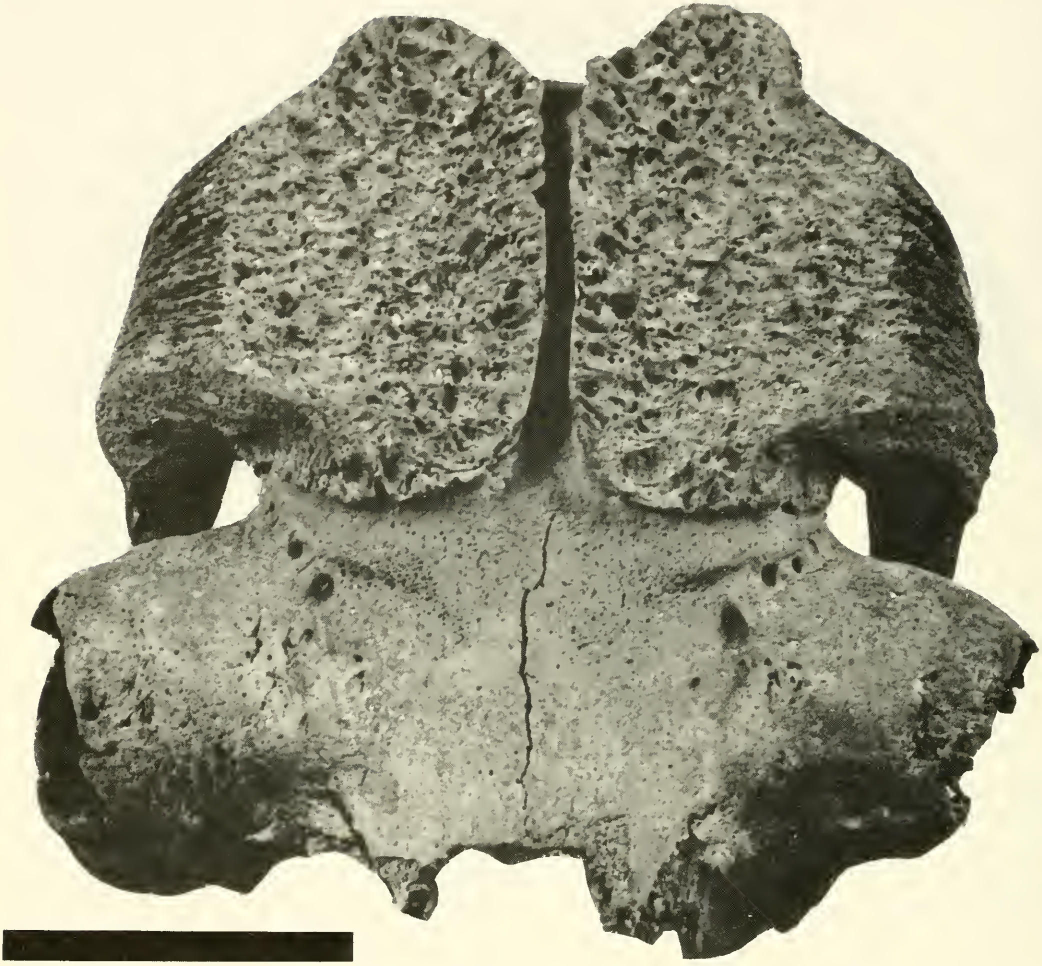

Fig. 5. *Ovibos moschatus*, unnumbered specimen, Alaska Fish and Game, (male) anterodorsal view. Bar represents 10 cm.

rounded horn cores of *Bootherium*.

The horn cores exhibit a sculpturing that is very similar, if not identical, to several male *Symbos* specimens in the Utah Division of State History and Utah Museum of Natural History collections. Evident are a series of grooves which tend to wrap around in a counterclockwise direction as they descend down the horn core. Although not continuous, the grooves extend to the very tip of the cores (Figs. 1, 4).

The thickness of the cranial roof does not vary appreciably anteriorly (62 mm) or posteriorly (58 mm) from the horn cores. However, there is a distinct difference in the type of bone present in the cranial cap. Anterior to the horn cores, the cranium is composed of highly vacuolate bone. Posterior, the entire cranial roof is constructed of finely cancellous bone. This spongy bone is similar to that observed on male *Symbos* skulls but absent in specimens of *Bootherium bombifrons*.

DISCUSSION.—Harington (*fide* Kurten and Anderson 1980:332) believed the evidence supporting the female *Symbos* designation of the type specimen of *Bootherium sargenti* quite compelling. He noted, according to Kurten and Anderson,

> the similar basic confirmation of the horn-cores, the smaller size of the cranium, and the broad space between the horn-core bases parallels the differences between male and female *Ovibos moschatus*.

The sexual dimorphism in modern specimens of *Ovibos moschatus* is clearly noted in

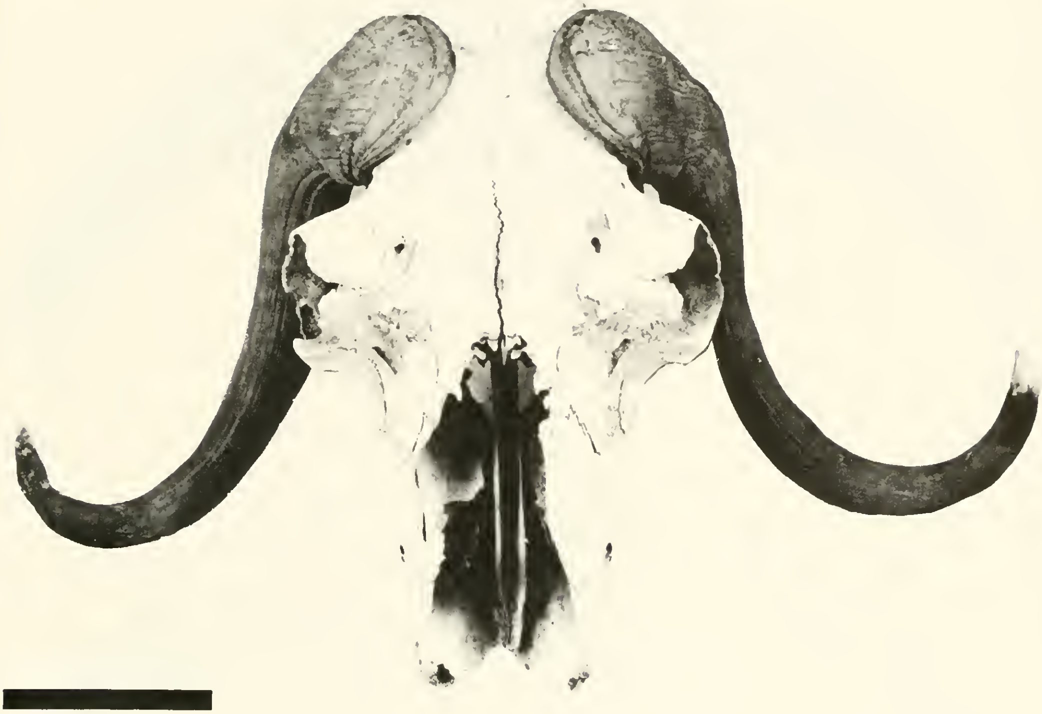

Fig. 6. *Ovibos moschatus*, unnumbered specimen, Alaska Fish and Game, (female) anterodorsal view. Bar represents 10 cm.

cleaned skulls, although it is not apparent in living specimens. In male specimens of *Ovibos* "the base of the horn-core is enlarged and expanded over a great part of the frontals and parietals, on which large exostoses are developed" (Lonnberg 1900). However, there is a very characteristic medial groove that separates the horn cores (Fig. 5). In examining skulls of female *O. moschatus*, we have found that the horn cores are much more widely separated at the bases and the frontals are nearly smooth between the horn cores. There are no large exostoses developed (Fig. 6). In addition, the horn cores of the females are not as massive as those of the male. This difference then, between male and female *O. moschatus* specimens, is very similar to the morphological differences noticed in specimens of "*Bootherium sargenti*" and *Symbos cavifrons*.

UVP 083 is almost identical to KUVP 61635, a set of horn cores and associated partial skull from Natural Trap Cave in northwestern Wyoming (Neas, personal communication 1981) (Fig. 7). This latter specimen has stockier and somewhat shorter horn cores than UVP 083 but morphologically agrees in all other details. The sculpturing is similar, the cancellous bone is present, the horn cores slightly overlap the frontals, the frontals are smooth between the horn cores, and a slightly elevated mid-frontal ridge is present. Neas (personal communication 1985) believes that the Natural Trap cave specimen may represent a female *Symbos*.

The Wyoming (KUVP 61635) and Idaho specimens (UVP 083, LACM 6671) also appear to be very similar, if not almost identical, to the type of *Bootherium sargenti* from Michigan (GRPM 114233101) described by Gidley (1908) (Figs. 8, 9). Therefore, we agree with the suggestions of Allen (1913), Hibbard and Hinds (1960), Semken, Miller, and Stevens (1964), and Kurten and Anderson (1980) and hereby propose that *Bootherium sargenti* (GRPM 114233101), *B. appalachicolus* (ANSP 29, placed in synonymy with *B. sargenti* by Ray, 1966a), *B. brazosis* (TAMC 2553, placed in synonymy with *B. sargenti* by Ray, 1966b), *B. nivicolens* (USNM 2324,

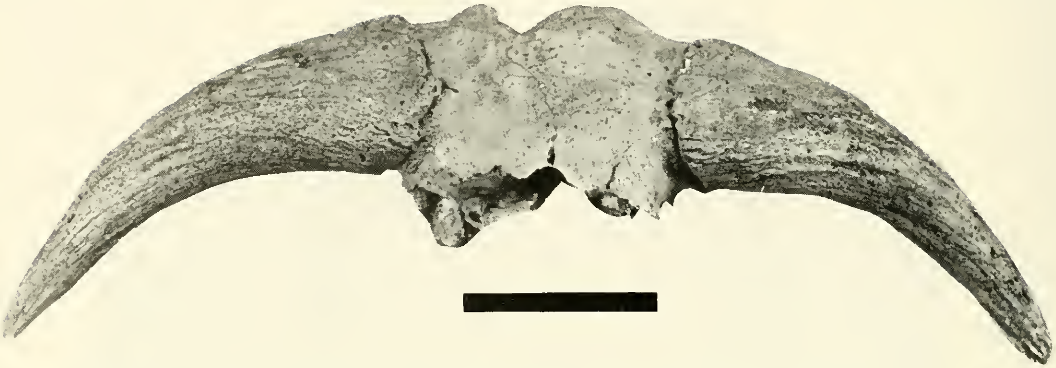

Fig. 7. *Symbos cavifrons*, KUVP 6135, anterodorsal view of horn cores. Bar represents 10 cm.

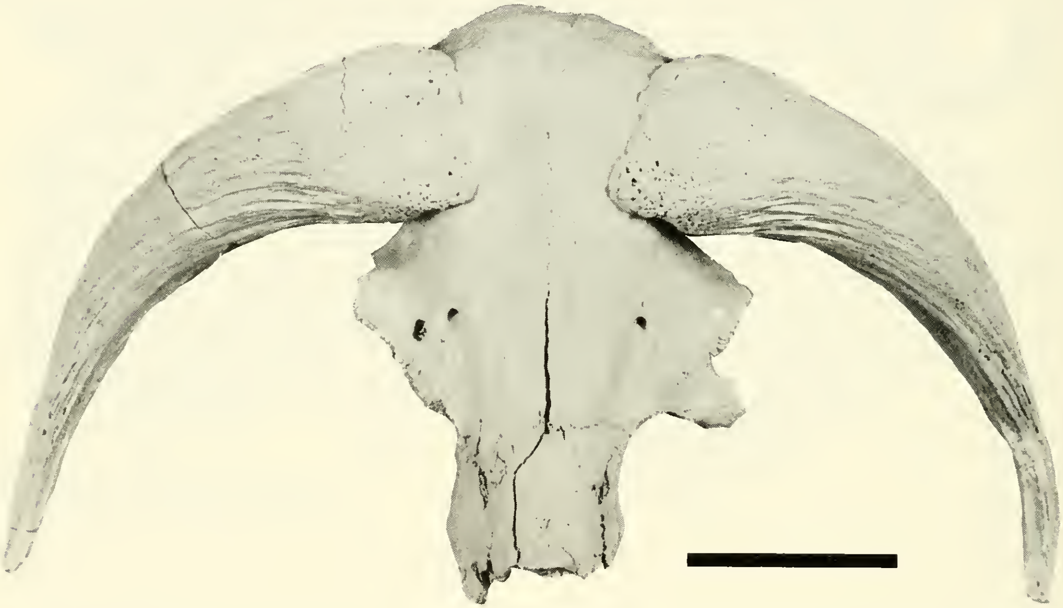

Fig. 8. "*Bootherium sargenti*" (=*Symbos cavifrons*), USNM 23488 (cast), original GRPM 11 423 3101, dorsal view. Bar represents 10 cm.

placed in synonymy with *B. sargenti* by Harington, written communication 1978), and *Bootherium* sp. (LACM 6671, White 1985) be included with *Symbos cavifrons* as sexual dimorphic forms. Other specimens would also include KUVP 61635 (Neas, personal communication 1985), BYUVP 9278 (Nelson, unpublished information), and the Idaho specimen in this discussion, UVP 083.

STATUS OF *BOOTHERIUM*

Kurten and Anderson (1980) and Harington (written communication 1978) believe that *Bootherium bombifrons* is a valid taxon "presuming the type . . . does not represent an abnormal individual." A reexamination of the Pleistocene specimens from Utah confirms the taxonomic validity of this determination.

USU 3529 is a partial cranium collected from the late-Pleistocene shoreline deposits of Lake Bonneville in northern Utah (Nelson and Madsen 1978) (Fig. 10). Although the skull is incomplete, there are sufficient diagnostic characters present to assign it to *Bootherium*. The horn cores stand out from the skull on a pedicel and display a distinct burr at the proximal border. They are

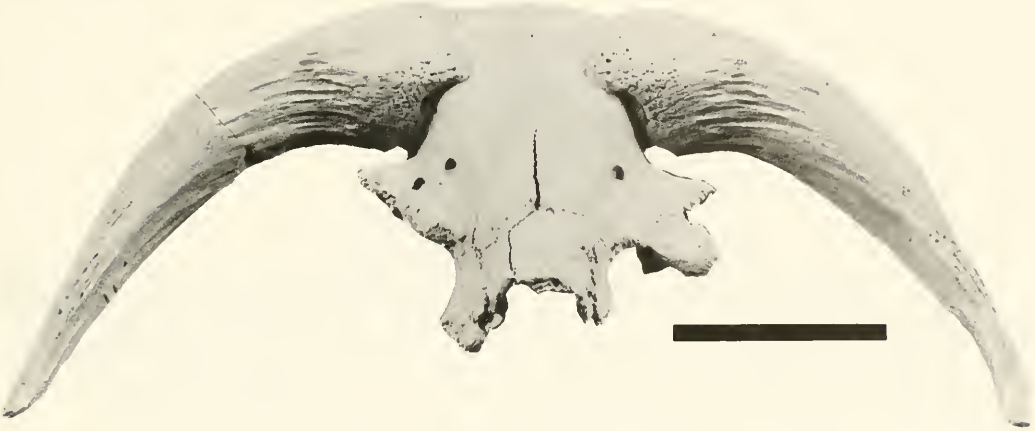

Fig. 9. "*Bootherium sargenti*" (=*Symbos cavifrons*), USNM 23488 (cast), original GRPM 11 423 3101, anterodorsal view. Bar represents 10 cm.

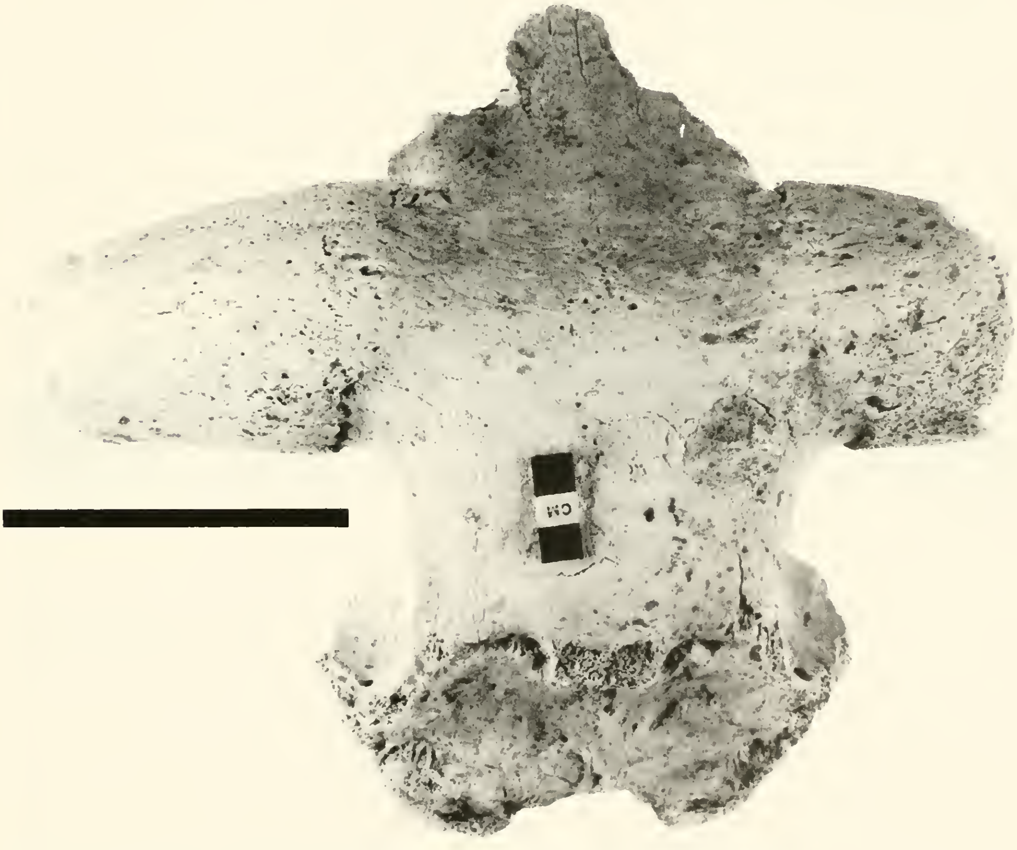

Fig. 10. *Bootherium bombifrons*, USU 3529, posterodorsal view. Bar represents 10 cm.

rounded in cross section and are unflattened dorsally near their bases. An exostosis and cranial sulcus are lacking, and the frontals between the horn cores are smooth. Perhaps, and most importantly, there is a very abrupt posteroventral slope of the dorsal outline of the skull posterior to the horn cores. This sloping area is a very diagnostic feature on the

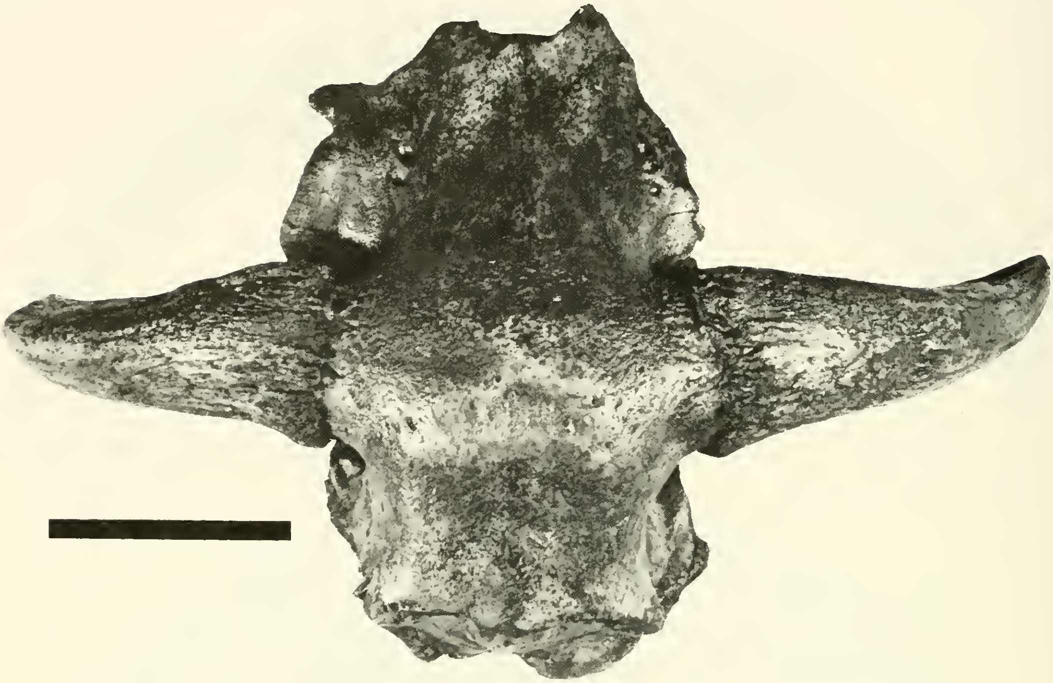

Fig. 11. *Bootherium bombifrons*, USNM 215066 (cast), original ANSP 2994, posterodorsal view. Bar represents 10 cm.

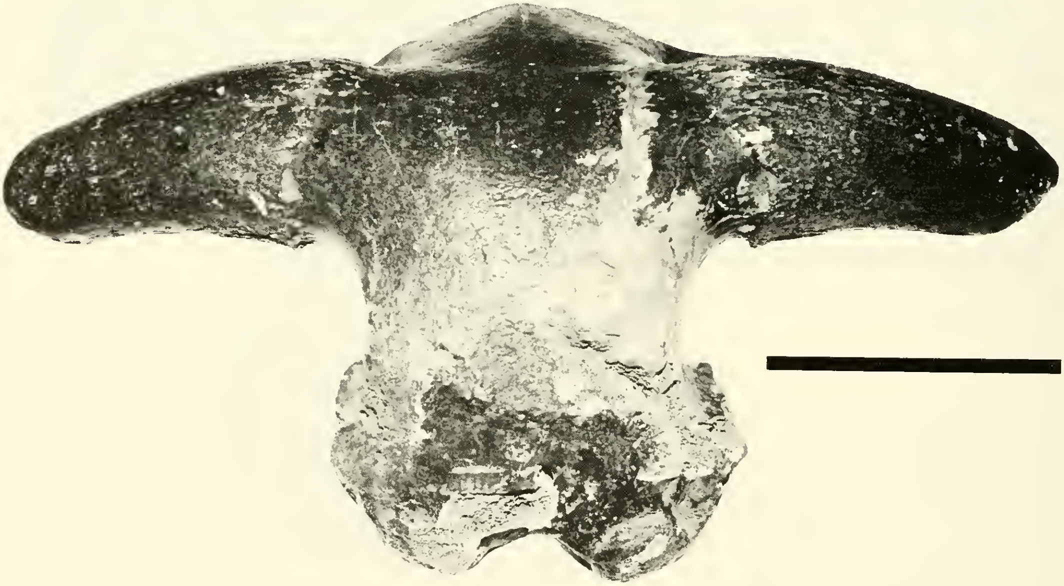

Fig. 12. *Bootherium bombifrons*, BYUG 834, posterodorsal view. Bar represents 10 cm.

type specimen of *B. bombifrons;* the horn cores seem to be placed on the summit of the skull very similar to the condition in goats and sheep, but unlike *Symbos* (Fig. 11).

Although the ventral part of this skull is abraded, sufficient detail is present to permit identification of the characteristic basioccipital-basisphenoid area. In *Bootherium* the

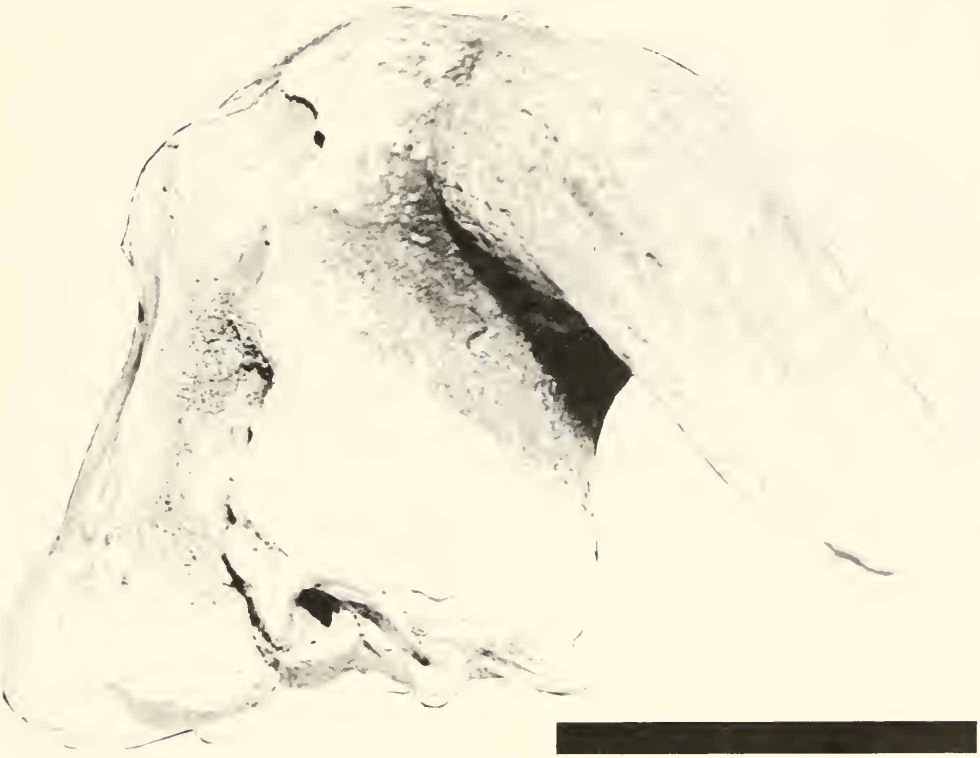

Fig. 13. *Bootherium* sp. indet., IMNH 17124, right lateral view. Bar represents 10 cm.

proximal end of the basisphenoid is dorsally deflected from the basioccipital at a very low angle (less than 20 degrees). In *Symbos* this deflection is greater than 35 degrees (White, personal communication 1984).

A second *Bootherium* skull from Utah (BYUG 834) is quite similar to USU 3529 in most characteristics (Fig. 12). The single, major difference is in the length of the sloping skull cap posterior to the horn core attachment. In BYUG 834 this length is only about 90% of the length of USU 3529. However, this difference may be attributable to post mortem abrasion of the skull rather than to pathology, individual variation, or sexual dimorphism.

Both Utah specimens (BYUG 834 and USU 3529) of *Bootherium* may now be assigned with certainty to *B. bombifrons*. They, but especially USU 3529, are almost identical to the type specimen of *B. bombifrons* in size and morphological characteristics. A second specimen of *Bootherium* in the Brigham Young University collections could not be located (Nelson and Madsen 1978), but photographic evidence suggests that it too is *B. bombifrons*. UUVP 8532, described by Nelson and Madsen (1978), also appears assignable to *B. bombifrons*, but post mortem abrasion of the specimen makes this latter identification more tenuous.

A specimen, IMNH 17124, which was collected from Bannock County, Idaho, and described by White (1985) as *Bootherium* sp., is difficult to place specifically (Fig. 13). It exhibits all of the characteristics of *Bootherium bombifrons* (see White 1985 for a description), with the exception of the length of the skull cap posterior to the horn core attachment (Fig. 14). In IMNH 17124 the cranial cap slopes abruptly downward at a much greater angle than in *B. bombifrons*. In addition, the length of the cranium posterior to the horn cores is 30% shorter than comparable specimens of *B. bombifrons*. This specimen may represent a pathological individual, a new species of *Bootherium*, an individual variant, or a sexual opposite from that of the type specimen of *B. bombifrons*. The gracile nature of this specimen suggests the latter choice, with IMNH 17124 representing a female.

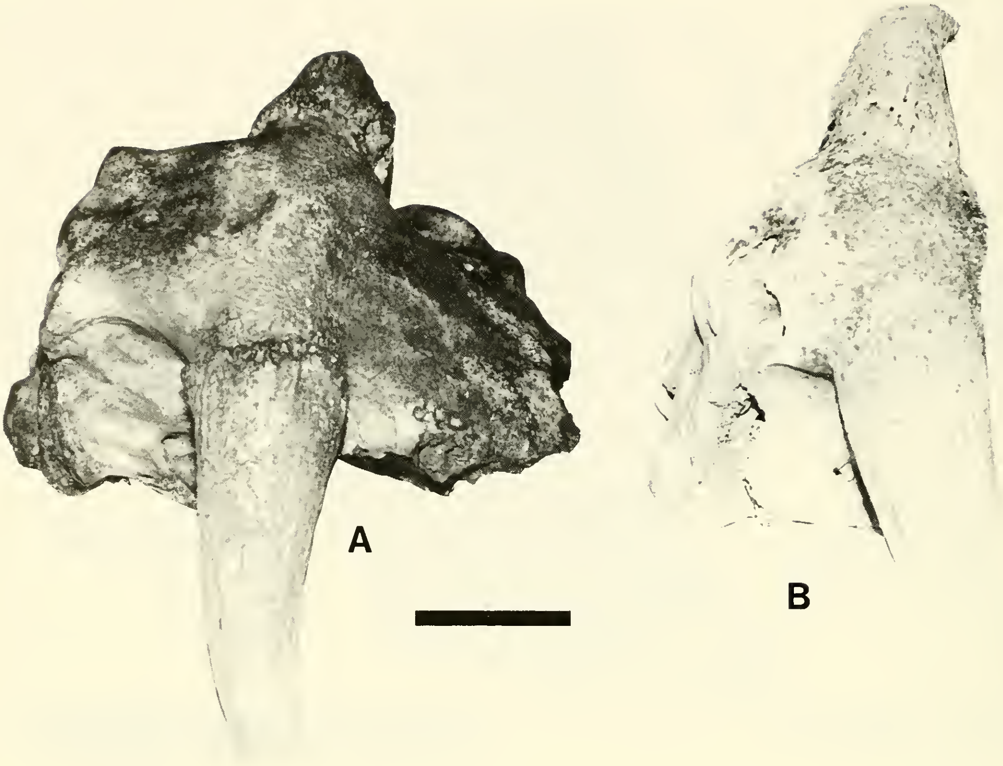

Fig. 14. A, *Bootherium bombifrons*, USNM 215066 (cast), original ANSP 2994, right dorsolateral view; B, *Bootherium* sp. indet., IMNH 17124, right dorsolateral view. Bar represents 10 cm.

SUMMARY

In summary, we assert that UVP 083 is inseparable from *Bootherium sargenti*, which in turn is placed in synonymy with *Symbos cavifrons*. These are sexual dimorphic forms, and it is likely that the typical *S. cavifrons* specimens are males whereas the "*B. sargenti*" forms are females. *Bootherium bombifrons* is a valid taxon and is probably not closely related to *S. cavifrons*.

ACKNOWLEDGMENTS

We could not have completed this paper without the counsel and help of John White and Clayton Ray. Robert Purdy of the Smithsonian Institution graciously loaned us casts of "*Bootherium sargenti*" and *B. bombifrons*, while John Neas of the University of Kansas furnished a cast of the Natural Trap specimen. Wade Miller (BYUG), Bill Akerston (IMNH), Greg Ostrander (KUVP), Dave Liddell (USU), Charles Repenning (USGS), Tim Smith (Alaska Fish and Game), and George Corner (Nebraska State Museum) made specimens in their care available for study. We also gratefully acknowledge the many discussions with other ovibovine enthusiasts including Jerry McDonald, John Neas, Dick Harington, John White, Clayton Ray, Lee Stokes, and George Corner. The financial support for this project was shared to some degree by the Utah Division of State History and DINOLAB, Salt Lake City, Utah, and Fort Hays State University, Hays, Kansas.

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EFFECTS OF LOGGING ON HABITAT QUALITY AND FEEDING PATTERNS OF ABERT SQUIRRELS

Jordan C. Pederson[1], R. C. Farentinos[2], and Victoria M. Littlefield[3]

ABSTRACT.—In 1973 a timber harvest of ponderosa pine (*Pinus ponderosa*) was conducted in an area southeast of Monticello, Utah, that is inhabited by Abert squirrels (*Sciurus aberti*). Abert squirrel dietary habits, foraging patterns, and population densities were compared in the timber harvest area and in an adjacent nonharvested area. Squirrel feeding patterns and preferences were visually determined by physical evidence of past feeding. Live-trapping and field-marking of animals were used to determine population density and trends in the two areas. Squirrels fed in only 26.3% of sampled plots on the timber harvest areas, while 42.7% of the uncut area plots showed use ($P < 0.001$). Trap days per catch were higher on the harvested area ($P < 0.01$). Similar differences in hypogeous fungi feeding sites between the two study sites were also recorded ($P < 0.01$). Thus, clearcut timber harvest of ponderosa pine did negatively affect Abert squirrels. To minimize long-term effects on squirrels, timber should be harvested in small, selective blocks (< 20 acres) rather than in large-scale areas (> 50 acres) by clear-cut methods commonly employed by management agencies.

Mammalian food habits studies have been conducted in several ways: *ad libitum* feeding of captive animals, fecal analysis, sacrificing free-ranging animals and inventorying the stomach contents, stomach pumping, and field observations of animals' feeding behaviors. All methods have distinct advantages and disadvantages.

Captive feeding allows control of the animals' environment and quantitative/qualitative regulation of intake, but the results may not validly apply to wild populations. Shooting or kill-trapping of individuals, together with subsequent stomach content examination, assumes that a large enough sample has been taken to represent the food habits of that population. The removal of individuals from a small population may also be disadvantageous. The use of observational data is based on the assumption that the observations are representative of the natural habits and that all food items can be properly identified by the observer. In this study, food habits and preferences of free-ranging Abert squirrels (*Sciurus aberti*) were determined by examining physical evidence resulting from squirrel feeding. Such evidence is easily recognized and consists of ground litter disturbance (resulting from digging for fungi), ponderosa pine (*Pinus ponderosa*) cone removal and descaled cone litter, large numbers of terminal needle bunch clippings found under selected ponderosa pine trees, and debarked twigs from ponderosa pine branches (Pederson et al. 1976).

Abert squirrels (*Sciurus aberti* subspp. and *Sciurus aberti kaibabensis*) are dependent on currently available food items since they do not cache foods for later feeding (Keith 1956, 1965, Stephenson 1975). Their diet includes acorns (*Quercus gambelii*), ectomycorrhizal (hypogeous) fungi, and seeds of dwarf mistletoe (*Arceuthobium vaginatum*). Ponderosa pine products include cambium ("inner bark") buds, cones, and seeds (Trowbridge and Lawson 1942, Keith 1956, 1965, Reynolds 1966, Larson and Schubert 1970, Heidmann 1972, Patton 1974, 1975, Stephenson 1975, Rasmussen et al. 1975). The abundance and growth of many of the foods consumed by Abert squirrels are affected by weather conditions.

The current study was undertaken to determine whether timber harvest of ponderosa pine affects the availability of Abert squirrel foods (e.g., inner bark, cone seeds, fungi, etc.). Effects of timber harvest on squirrel densities, foraging patterns, movements, and/or time-energy budgets were also examined.

Objectives of the study were to:

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[3] University of Minnesota, Morris, Minnesota 56267.

1. Quantify dietary changes on a seasonal basis.
2. Correlate dietary changes with food item availability.
3. Determine how seasonal changes in diet and food item availability affect foraging patterns.
4. Analyze relative energy content of various food items, i.e., calorie content of ponderosa pine seeds vs. inner bark vs. buds, etc.

STUDY AREA

The study area is in southeastern Utah on the Monticello Ranger District of the Manti-LaSal National Forest. Lying in the Bulldog-Verdure drainages of the Abajo Mountains, it is approximately 12 k (8 mi) southeast of Monticello, Utah. In 1973 the Bulldog area was part of a timber harvest program by the U.S. Forest Service. The adjacent Verdure area served as a nonharvested control in a three-year Utah Division of Wildlife Resources study conducted to determine the short-term effects of timber harvest on Abert squirrels (Pederson et al. 1976). The Verdure and Bulldog sites, each 56 ha (140 ac) in size, were studied simultaneously.

METHODS AND PROCEDURES

For both the harvested and unharvested areas, two types of food-related data were collected: (1) data on *actual* squirrel food use, and (2) data that reflected *potential* food available.

1. Data on actual Abert squirrel food use was obtained quarterly (April 1977–December 1979) from 300 circular, random-sampled, 10-m^2 plots on each study area. Descaled ponderosa pine cones, peeled ponderosa pine twigs, hypogeous fungi digs, use of dwarf mistletoe, and other feeding evidence were counted and recorded for each plot.

Information was also collected on the number of plots in which any feeding activity occurred on either area. The food item used was also recorded. Foods eaten by Abert squirrels were collected and tested for nutrient and caloric content. Foods were tested for percent moisture, Kjeldahl determination for protein, ash content, and Soxhlet extraction of lipids as described in the Official Methods of Analysis manual (1975).

2. Potential food available (i.e., current-year production of food items) was obtained by surveying 300 randomly selected plots each September and estimating production of ponderosa pine cones and Gambel oak acorns. These production estimates were tied to the food-use plots in the following manner: The closest ponderosa pine tree and Gambel oak tree to each food-use plot were observed through 7 x 35 binoculars. Cones or acorns on a quarter of the tree were counted and multiplied by four to obtain an estimate of the current year's cone and acorn production. These production estimates were converted into a class code using the following key:

Acorn and Ponderosa Pine Cone Production Key

Class	Prod. est./tree (cones or acorns)
0	none
1	1 – 25
2	26 – 50
3	51 – 100
4	101 – 200
5	201 – 400
6	401 – 600
7	601 – 800
8	801 – 1,000+

Data were also collected on the amount of ground and litter disturbance caused by logging activity that occurred between 1973 and 1975. Litter depth was recorded on every tenth plot for both logged and unlogged areas when the ground was free from snowcover. This was converted into a class code as follows:

Litter Depth Key (pine needles to mineral soil)

Class	Depth (cm)
0	none (bare ground)
1	1 – 5
2	6 – 10
3	11 – 16
4	17 – 20+

Live-trapping and field observation techniques were used to aid in the evaluation of responses of squirrels to timber harvest. Squirrels were trapped using Tomahawk live traps, No. 203, 6 x 6 x 24 inches (Tomahawk Live Trap Company, Tomahawk, Wisconsin). The traps were positioned throughout the study areas in eight locations most often frequented by squirrels. These areas were determined by the presence of recent squirrel sign, nest locations, and actual observations of squirrels. Traps were placed in known or sus-

TABLE 1. Utah Abert squirrel food use data, 1977 through 1979.

YEAR AREA Month	Ponderosa pine clips no.	Use %	Fungi digs no.	Use %	pine peeled cones no.	Use %	Mistletoe	Use %
1977								
BULLDOG								
July	58	59	0	0	39	40	0	0
Sept.	206	64	46	14	70	22	1	T
Dec.	58	59	0	0	39	40	1	T
VERDURE								
July	467	76	91	15	57	8	0	0
Sept.	67	21	125	40	124	39	1	T
Dec.	57	75	5	6	15	19	1	T
1978								
BULLDOG								
Feb.	140	100	0	0	0	0	0	0
April	264	96	5	2	6	2	1	T
July	189	72	62	23	13	5	0	0
Sept.	238	100						
Dec.	396	100						
VERDURE								
Feb.	131	100	0	0	0	0	0	0
April	486	100	0	0	1	T	0	0
July	183	39	280	60	3	0.5	3	0.5
Sept.	197	100						
Dec.	285	100						
1979								
BULLDOG								
Feb.	276	100						
April	301	100						
VERDURE								
Feb.	287	100						
April	351	100						

pected centers of squirrel activity to establish home ranges (Hayne 1949). These activity centers were determined during a previous study (Pederson et al. 1976). Each trap was baited with both roasted peanuts and peanut butter. Each squirrel trapped was placed in a Plexiglas cone and then anesthetized with methoxyflurane (Metofane, Pitman-Moore, Inc., Fort Washington, Pennsylvania) using Barry's (1972) method on gray squirrels. The anesthetized squirrel was removed from the cone for measuring and tagging. Sex, age, weight, rectal temperature, tail length, total length, length of hind foot, ear and ear tassel length (if present), coloration, presence of parasites,, and any abnormalities were recorded. Parasites were collected for later identification. A careful record was kept on the time required to relax, time under, and recovery time from anesthesia.

While the animal was still anesthetized, it was numbered with aluminum rabbit tags (National Band and Tag Co.) placed through each ear and secured with 3/8-inch (.94-cm) celluloid colored washers for later field and in-trap identification. A backup identification system insured future identification in case of tag loss; it consisted of a colored collar, made from TY-RAP CABLE ties (#TY-525 M. manufactured by Thomas Betts Co., Elizabeth, New Jersey), which was fastened around the squirrel's neck. Each collar was factory numbered as an additional aid in identifying recaptured squirrels.

RESULTS AND DISCUSSION

Food-Use Data

A comparison of overall feeding activity between the two study areas during the two years shows that squirrel feeding occurred in 26.3% of the harvested Bulldog plots. Feeding was recorded in 42.7% of the nonharvested Verdure plots. The difference is signif-

TABLE 2. Utah Abert squirrel trapping record, 1977–1978.

	Bulldog					Verdure				
Month	New squirrels caught	Total catches	Trap days	Trap days per new catch	Trap days per catch	New squirrels caught	Total catches	Trap days	Trap days per new catch	Trap days per catch
1977										
April	7	9	58	8.28	6.44	14	15	58	4.14	3.86
July	1	2	42	42.00	21.00	4	10	52	13.00	5.20
September	1	1	24	24.00	24.00	2	4	24	12.00	6.00
December	3	6	72	24.00	12.00	2	18	72	36.00	4.00
TOTAL	12	18	196	16.33	10.88	22	47	206	9.36	4.38
1978										
February	0	4	36	0	9.00	0	1	36	0	36.00
April	4	6	21	5.25	3.50	1	9	21	9.00	2.33
September	1	10	32	10.00	3.20	6	17	32	5.33	1.88
December	0	21	22	0	22.00	0	2	22	0	11.00
TOTAL	5	41	111	22.20	2.36	7	29	111	15.85	3.82
Two-year summary	17	59	307	18.05	5.20	29	76	317	10.93	4.17

icant at the $P < 0.01$ level (Table 1). This difference is also significant when the data are compared separately by year. The lower incidence of feeding activity in the area where ponderosa pine was harvested shows that some degradation of Abert squirrel habitat has occurred. The difference in feeding activity suggests lower population numbers and apparently lower recruitment of young in the Bulldog area. Squirrel movement from Bulldog to Verdure for feeding was documented. Evidence of lowered population numbers in the Bulldog area is shown in both the higher number of trap days required for catching new squirrels and in lower total squirrel catches (Table 2).

Feeding activity in both areas was of four specific types: ponderosa pine bark (needle bunch clips), ponderosa pine seeds (cones), dwarf mistletoe, and hypogeous fungi (digs). Data collected during the study show the majority of the feeding was on ponderosa pine inner bark or cambium tissue (Table 1). This contrasts with other reports that twig feeding occurs mainly during winter months (Keith 1965, Stephenson 1975, Rasmussen et al. 1975). Frequent use of ponderosa pine seed was recorded only in 1977 and coincided with a very large cone crop (Table 1). Dwarf mistletoe was used only in trace amounts. Stephenson (1975) also reported that squirrels in Arizona used very little mistletoe. The use of ectomycorrhizal fungi was highest during July and September and was a direct reflection of summer precipitation (Table 1).

A significantly higher number of feeding activity occurrences of hypogeous fungi were recorded for the uncut Verdure area. Fungi digs in the Bulldog area were 176, with 549 at Verdure. This difference is significant at the $P < 0.001$ level. Hypogeous fungi grow beneath a layer of ponderosa pine needles having a depth greater than 5 cm. Bulldog litter depth greater than 5 cm was present in only 23.3% of the plots, while this depth at Verdure occurred in 40.2%. This is also the percent hypogeous fungi digs found between the two sites (Table 1). Bulldog plots show 15.9% bare ground and Verdure 8.2%. Disturbance to ground cover by logging activity was found in 38.4% of the plots examined ($N = 1{,}250$). The opening of the upper canopy cover by timber harvest and accompanied logging activity has removed and reduced the litter cover and depth, thus reducing the microclimate necessary for production of hypogeous fungi, a sought-after and preferred food of the Abert squirrel. Stephenson (1975) reports that fungi were the "most important item on an annual basis, by volume and frequency of occurrence." He found fungi in the diet every season of the year, comprising as much as 91.9% of the summer diet. In addition, hypogeous fungi grow only on the roots of live ponderosa pine. Logging that kills the root system will also obviously cause the loss of this food source to Abert squirrels (Ure and Maser 1982).

TABLE 3. Chemical and caloric content on Abert squirrel foods in Utah, 1977–79.

Date collected	Food item	Moisture %	Protein %	Fats & oils %	Ash %	Calories per g
1977						
22 April	Pipo* staminant cone	71.92	4.46	4.84	4.07	
22 April	Pipo seed	36.89	4.05	5.47	7.95	
4 July	Pipo cambium	44.12	4.62	7.65	4.34	
4 July	Pipo seed	8.77	9.48	11.59	4.63	
4 July	Mistletoe	56.74	6.60	2.14	10.52	
22 Sept.	Mistletoe	59.14	6.23	2.40	4.63	
22 Sept.	*Boletus*	87.99	25.06	5.03	9.68	
22 Sept.	Fairy ring	72.76	17.75	6.74	34.32	
22 Sept.	Cantlarelaceae	72.35	13.79	1.72	25.23	
22 Sept.	*Russula*	87.61	16.61	5.50	16.14	
22 Sept.	Pipo seed	62.44	5.06	11.89	31.22	
3 Nov.	Pipo seed	19.76	6.43	11.08	14.14	5,479.0
2 Dec.	Mistletoe	54.69	6.73	1.16	4.48	2,586.1
2 Dec.	Pipo cambium	47.74	2.07	3.40	10.16	2,454.4
1978						
20 Feb.	Pipo cambium					
	Bulldog	48.08	1.65	3.84	8.20	4,155.9
	Verdure	52.21	1.56	5.39	5.04	4,212.9
16 April	Pipo cambium					
	Bulldog	44.68	1.80	4.59	9.34	4,039. 5
	Verdure	51.28	2.40	3.93	6.89	3,889.0
16 April	Pipo mistletoe	60.13	7.24	2.22	5.76	4,669.5
29 May	Pipo cambium (Bulldog)					
	Feed tree	47.85	2.10	4.51	5.05	4,146.0
	Nonfeed tree	48.33	2.09	4.22	7.80	4,195. 3
	Pipo buds	76.70	7.29	3.36	3.01	4,384.9
	Pipo mistletoe	62.30	6.60	1.91	5.16	4,999.2
	Juos mistletoe	60.61	8.51	2.16	13.06	4,195.3
4 July	Pipo cambium (Bulldog)					
	Feed tree	48.97	2.20	6.91	8.68	3,932.0
	Nonfeed tree	46.92	1.78	5.41	9.21	3,724.9
	Pipo mistletoe	64.92	5.45	1.36	5.30	4,793.0
22 Sept.	Pipo cambium (Bulldog)					
	Feed tree	51.90	2.70	2.80	9.30	—
	Mistletoe	59.74	5.20	1.15	4.83	—
	Acorns	46.63	5.53	.04	1.28	4,220.0
30 Dec.	Pipo cambium (Bulldog)					
	Feed tree	43.34	2.34	.85	2.84	3,765.0
	Nonfeed tree	49.66	2.41	1.87	2.41	3,955.0
1979						
11 Feb.	Pipo cambium (Bulldog)					
	Feed tree	51.23	2.83	1.13	6.38	4,150.0
	Nonfeed tree	51.23	2.68	.81	9.44	3,860.0
1 April	Pipo cambium (Bulldog)					
	Feed tree	53.86	2.56	1.78	5.58	4,498.0
	Nonfeed tree	55.29	2.38	1.72	5.48	4,254.0

*Pipo = ponderosa pine = *Pinus ponderosa*

The difference in feeding activity might be accounted for in lower population numbers and lower recruitment of young in the Bulldog area or a movement from Bulldog to Verdure for feeding.

Food Chemical Analysis

The moisture content of Abert squirrel foods ranged from a low of 8.77% in ponderosa pine seed to a high of 87.99% in boletus fungi

(Table 3). Ponderosa pine inner and outer bark showed a 49.30% moisture content for the study period (range = 43.34–55.29%). Mistletoe was the most consistent in percent moisture with a mean of 59.8 and a range of 54.69–64.92.

Protein expressed on a dry-matter basis was highest in the fungi species (*Boletus* spp. averaged 25.06%; *Marasmius oreades*, 17.75%; *Cantorelaceae*, 13.79%; and *Russula* spp., 16.61%). These high protein levels for fungi are consistent with the Abert squirrel food habits study by Stephenson (1975). Southwestern dwarf mistletoe was relatively low in percent protein with a mean of 6.30 and a range of 5.20–7.24 (Table 3).

Ponderosa pine cambium (inner bark) was very low in percent protein. Thirteen samples collected during the study period yielded a mean of 2.28% (range = 1.56–4.62%) (Table 3). These data are similar to those of 1.5–3.2% reported by Pederson and Welch (1985). Inner bark, long thought to be the mainstay of the Abert squirrel diet, had a very low protein level (Table 3). Stephenson (1975) found inner bark in the diet throughout the year, but in significant quantities only in winter months. During very dry summers we found that feeding activity was as high as 76% on ponderosa pine inner bark (Table 1). The high moisture level of inner bark (averaging 49.30%) may account for its use as a water source in the diet.

A study by Stephenson and Brown (1980) shows an annual mortality of 66% in a year with snowcover of 10 cm or more for 85 days. Their finding shows a positive correlation of the number of days of snow depth greater than 10 cm with the annual mortality rate of Abert squirrels in Arizona. During these periods of 10 cm or more of snow, squirrels were forced to eat only bark with its low protein content when higher protein foods such as fungi were unavailable for use. If deep snow lasted long enough, the squirrels could develop a severe nitrogen deficiency that could greatly increase the mortality rate (Pederson and Welch 1985). During snow-free months if hypogeous fungi habitat is reduced, this source of protein is unavailable to squirrels and the population declines.

SQUIRREL WEIGHTS

The weights of squirrels differed between areas. Those captured in the Bulldog timber harvest area weighed an average of 658.8 grams; those from Verdure averaged 670.8. Males weighed 640.2 grams and 653 grams, respectively. These data do not show significant statistical differences but suggest a trend to better body condition on the nonharvested Verdure area.

ECTOPARASITES

Captured squirrels were combed and external parasites collected. Two species of flea were recovered and identified. On 21 April 1977 a female *Monopsyllus eumolpi* was collected from an adult male Abert squirrel captured in the Verdure area. The same species was also found on another adult male Verdure squirrel on 2 July 1977. On 8 September 1977 a large male *Hystrichopsylla dippiei* was removed from an adult female squirrel trapped in the Bulldog study area. During the same time period an adult female Abert squirrel was captured, and a male and female *Dermacentor andersoni* were removed from her ears. The presence of external parasites did not appear to affect body condition or health of Abert squirrels on either area.

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PARASITES OF THE CUTTHROAT TROUT, *SALMO CLARKI*, AND LONGNOSE SUCKERS, *CATOSTOMUS CATOSTOMUS*, FROM YELLOWSTONE LAKE, WYOMING

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Abstract.—Twenty-five cutthroat trout (*Salmo clarki*) and eight longnose suckers (*Catostomus catostomus*) from Yellowstone Lake, Wyoming, were collected and examined for parasites in 1985. Cutthroat trout had at least six different species of parasites that included both protozoans and helminths. The greatest number of parasite species on one fish was nine. Parasites added to the known list for cutthroat trout from Yellowstone Lake, Wyoming, were: *Myxosoma* sp., *Diphyllobothrium ditremum*, *Diphyllobothrium dendriticum*, *Diplostomum baeri*, and *Posthodiplostomum minimum*. These data were compared with a previous survey (1971) and a checklist of parasites of cutthroat trout in North America. There are 17 species of parasites and two fungal species reported for cutthroat trout from Yellowstone Lake. *Trichophrya catostomi*, *Diplostomum spathaceum*, and *Ligula* sp. were observed in the small sample of longnose suckers.

Linton (1891a, 1891b) Woodbury (1932), and Bangham (1951) gave lists of parasites for Yellowstone Lake fishes, while Scott (1932, 1935, 1955), Simon (1935), and Cope (1958) published short reports concerning some of the known fish parasites from this lake. There is little information on the protozoan parasites from this locality. For instance, Bangham (1951) reported on one myxosporean from 2 of 291 cutthroat trout. Since the last comprehensive survey of parasites for a species of fish in Yellowstone Lake (Heckmann 1971), there have been brief reports on specific parasites. These articles emphasized the biology and host-parasite relationships of symbionts in the ichthyofauna of Yellowstone Lake (Otto and Heckmann 1984, Heckmann and Carroll 1985).

The scientific name currently used for the plerocercoids from cutthroat trout, Yellowstone National Park, is *Diphyllobothrium cordiceps* (Leidy 1871). Researchers in Canada and Norway have questioned the identification of the plerocercoids (Ching and Andersen, personal communication). There is a possibility of more than one type of plerocercoid in cutthroat trout, and there is the need to reevaluate the plerocercoids found in cutthroat trout from Yellowstone Lake.

The plerocercoids of *Diphyllobothrium* in Yellowstone Lake have received sporadic study since the early 1870s. Some of the natural hosts have been delineated. Prevalence and intensity in the second intermediate hosts (fishes) and natural definitive hosts (pelicans, gulls, and bears) have been determined by various researchers (Post 1971, Heckmann 1971). Life cycle experiments were completed using second intermediate hosts and natural definitive hosts as well as experimental hosts (dogs and domestic cats). Ova produced from the infected experimental hosts did not hatch. The first intermediate host for the cestode remains unidentified. Several aquatic zooplanktonic species in Yellowstone Lake are strongly suspected to be hosts in the life cycle.

Interest pertaining to the identification of the *Diphyllobothrium* plerocercoids has continued (Post 1971, Heckmann 1971, Andersen 1974, 1977, Otto and Heckmann 1984). The potential problem of human infections with plerocercoids of cutthroat trout in Yellowstone Lake, Wyoming, is of concern (Woodbury 1932, Post 1971, Otto and Heckmann 1984, Ruttenber et al. 1984). However, Woodbury (1935) claimed that the plerocercoids of *D. cordiceps* were not infective to man. Many cutthroat trout are discarded each year in Yellowstone National Park due to the unsightly infections of *Diphyllobothrium* larvae (Otto and Heckmann 1984).

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TABLE 1. Results of the 1985 survey for parasites of 25 cutthroat trout (*Salmo clarki*) from Yellowstone Lake, Yellowstone National Park, Wyoming.

Fish number	Total length (mm)	Weight (grams)	*Tricophrya*	Copepods	*Diplostomum** (metacercariae)	Plerocercoids** S = small, L = large	*Crepidostomum*	*Bulbodacnitis*	Comments (other parasites)
1	400	250	+++	+	+ (Retina, 11)	+ (S + L)	+	++	Two plerocercoid sizes
2	350	380	++	+	+ (Retina, 59)	+ (S)	+	++	Cestodes Leeches
3	345	450	++	+	+ (Retina, 15)	+ (L)	+	++	Cestodes deep in musculature
4	385	525	+++	0	+ (Retina, 100+)[a]	+ (S + L)	+	++	Cestodes in musculature
5	358	380	+++	+	+ (Retina, 28)	+ (S)	+	++	Small cestodes only, skin metacercariae
6	310	385	++	+	+ (Retina, 31)	+ (S)	+	++	Small cestodes only
7	329	410	++	+	+ (Retina, 18)	+ (S)	+	++	Small cestodes only, fungus
8	331	330	+++	0	+ (Retina, 21)	+ (S + L)	+	++	Plerocercoids frozen for electrophoresis Leeches
9	341	395	++	+	+ (Retina, 52)	+ (S + L)	+	++	Cestode in musculature
10	320	380	+++	+	+ (Retina, 41)	+ (S + L)	+	++	Myxosporidans in gill tissue
11	330	400	++	+	+ (Retina, 34)	+ (S + L)	+	++	Cestodes in musculature
12	348	285	++	+	+ (Retina, 100+)[a]	+ (S + L)	+	++	Cestodes in musculature
13	345	460	+++	+	+ (Retina, 100+)[a]	+ (S + L)	+	++	Cestodes in musculature
14	260	320	++	+	+ (Retina, 18)	+ (S + L)	+	++	Cestodes in musculature
15	300	360	+++	+	+ (Retina, 100+)[1]	+ (S + L)	+	++	Cestodes in musculature
16	305	355	++	+	+ (Retina, 50)	+ (S)	+	++	Small cestodes only
17	250	300	+++	0	+ (Retina, 21)	+ (S + L)	+	++	Leeches Small cestodes in musculature
18	300	345	++	+	+ (Retina, 36)	+ (S)	+	++	Copepods, small cestodes only
19	320	360	++	+	+ (Retina, 58)	+ (S + L)	+	++	Cestodes in musculature Leeches
20	250	310	+++	0	+ (Retina, 100+)[a]	+ (S + L)	+	++	Two cestode sizes, skin metacercariae
21	275	315	++	+	+ (Retina, 17)	+ (S + L)	+	+	Fungus, leeches
22	400	475	++	+	+ (Retina, 100+)[a]	+ (S)	+	++	Small cestodes only
23	200	265	+++	+	+ (Retina, 46)	+ (S + L)	+	++	Two cestode sizes
24	310	365	++	0	+ (Retina, 27)	+ (S + L)	+	+	Two cestode sizes
25	315	345	+++	+	+ (Retina, 100+)[a]	+ (S + L)	+	++	Cestodes in musculature

* The retina form is *D. baeri*, average number per eye in parentheses.

** There are two, possibly three, species of plerocercoids for cutthroat trout.

[a] When over 100 metacercariae are present, 100+ is recorded.

+ Indicates presence of parasite; the number of pluses gives indication of parasite burden.

TABLE 2. Summary of parasites observed for 25 *Salmo clarki*, cutthroat trout, from Yellowstone Lake, Wyoming, 1985.

Parasite group	Parasite species	Location of parasite	Prevalence (percent)
Ciliophora	*Trichophrya clarki*	Gill surface	100
Myxozoa	*Myxosoma* sp.	Skin, gills	4
Cestoda: Tapeworms	**Diphyllobothrium ditremum*	Muscle, viscera	100
	**Diphyllobothrium dendriticum*	Muscle, viscera	100
Digenea: Flukes	**Diplostomum baeri*	Retina of eye	100
	**Posthodiplostomum minimum*	Viscera	8
	Crepidostomum farionas	Intestine, gall bladder	100
Nematoda: Roundworms	*Bulbodacnitis scotti*	Intestine, pyloric caeca	100
Crustacea: Copepods	*Salmincola* sp.	Gills, mouth	80
Hirudinea: leeches	*Piscicola salmositica*	Gills, fins	16
Fungi	*Ichthyophonus* sp.	Skin surface	8

*larval stages, plerocercoids and metacercariae

This project had two main goals: (a) to conduct a survey for parasites in two common species of fish in Yellowstone Lake, cutthroat trout (*Salmo clarki*) and longnose suckers (*Catostomus catostomus*) and (b) to identify the species of plerocercoids found in *S. clarki*. The other helminth parasites of Yellowstone Lake fishes will be reviewed.

MATERIALS AND METHODS

Collections of cutthroat trout were obtained by net and trap at two sites on the east side of Yellowstone Lake during June 1985. Each fish was examined for external and internal parasites (immediately after death). The gills, fins, and viscera were removed and placed in finger bowls containing physiological saline. The organs were examined using a dissecting microscope. Each organ, the surface of each appendage, and the body surface were scraped with a scalpel, and the scrapings were placed in a depression slide containing a drop of physiological saline for examination using a compound microscope. Material from each scraping was also placed on glass slides, stained with methyl green-pyronin Y (Heckmann 1971), and observed at high magnification. Blood smears were prepared from the heart and peripheral circulatory system of each fish. Blood smears were air-dried, fixed with methyl alcohol, and stained with Giemsa. Each slide was examined with high-dry (430X) and oil-immersion (1,000X) objectives for 10 minutes. Data for each fish included length, weight, sex, location of sample, and parasites and their organ sites. Plerocercoids from the fish were (a) fixed in buffered 3% gluteraldehyde and AFA (acetic acid, formalin, alcohol) while (b) other plerocercoids were frozen. Whole mounts as well as preparations for scanning electron microscopy were made of the plerocercoids. Fixed specimens were sent to Drs. H. Ching in Canada and K. Andersen in Norway for identifications. Attempts to infect gerbils with the plerocercoids were made but were not successful.

Infected tissues were fixed in 10% buffered formalin for histological preparations to help ascertain host-parasite interaction. Standard methods (Davenport 1960) were used in preparing fixed tissue for microscopic observations. Paraffin-embedded gills were sectioned at 4–6 μm. After the sections were fixed to glass slides, the tissue was stained with Harris hematoxylin and eosin and a pentachrome stain for observation with a compound light microscope.

Samples of plerocercoids fixed with buffered 3% gluteraldehyde were processed through standard techniques for scanning electron microscopy (Dawes 1971). After liquid dehydration each specimen was subjected to critical-point drying. After the specimen was mounted on a holder, each plerocercoid was coated with gold in a CS minicoater sputter apparatus and viewed with an AM Ray

TABLE 3. Checklist of parasites observed for *Salmo clarki*, cutthroat trout, from Yellowstone Lake, Wyoming. Surveys conducted during 1969, 1970*, and 1985. A total of 288 fish were sampled.

		Percent infection		
Parasite group	Parasite species	Location of parasite	1969 1970	1985
Ciliophora:	*Trichophrya clarki*	Gills	95	100
	Trichodina sp.	Gills	0.4	0
Myxozoa:	*Myxosoma* sp.	Skin, gills	0	4
	Myxosporidan sp.	Gills	0.8	0
Flagellata:	*Haemogregarina* sp.	Blood cells	0.4	0
	Costia pyriformis	Gills	19	0
Cestoda: Tapeworms	***Diphyllobothrium ditremum*	Muscle, viscera	0	100
	***Diphyllobothrium dendriticum*	Muscle, viscera	0	100
	***Diphyllobothrium* sp.	Muscle, viscera	92	0
Digenea: Flukes	***Diplostomum baeri bucculentum*	Retina of eye	0	100
	***Posthodiplostomum minimum*	Viscera	0	8
	Crepidostomum farionas	Intestine, gall bladder	95	100
Nematoda: Roundworms	*Bulbodacnitis scotti*	Intestine, pyloric caeca	95	100
Acanthocephala: Spiny headed worms	*Neoechinorhynchus rutili*	Intestine	0.4	0
Crustacea: Copepods	*Salmincola* sp.	Gills, mouth	80	80
Hirudinea: leeches	*Piscicola salmositica*	Gills, fins	18	16
	Illinobdella sp.	Fins	0.4	0
Fungi: Mycota	*Ichthyophonus* sp. (*Saprolegnia*)	Skin surface	0	8

*Heckmann, R. A. 1971. Parasites of cutthroat trout from Yellowstone Lake, Wyoming. Prog. Fish Cult. 33: 103–106.
**larval stages, plerocercoids and metacercariae

TABLE 4. Results of the survey for parasites of eight longnose suckers (*Catostomus catostomus*) from Yellowstone Lake, Yellowstone National Park, Wyoming.

Fish number	Total length (mm)	Weight (grams)	*Trichophrya*	*Diplostomum** (metacercariae)	*Ligula intestinalis*	Comments (other parasites)
1 (male)	415	810	+	+ (Lens, 49)	1 (large)	*Ligula* 13.5 × 420 mm (contracted, gonad compression and atrophy
2 (male)	436	1250	+	++ (Lens, 100+) (Retina, 5–10)	—	Both lens and retina metacercariae
3 (female)	360	600	+	++ (Lens, 100+)	—	Opaque lens
4 (male)	432	1250	+	+ (Lens, 20)	—	Opaque lens center
5 (female)	310	400	+	+ (Lens, 20)	—	—
6 (female)	412	800	+	+ (Lens, 39)	—	—
7 (male)	440	950	+	+ (Lens, 10)	—	—
8 (male)	420	815	+	+ (Lens, 35)	1 (large)	*Ligula* large

*The lens form is *D. spathaceum*.

1000, a high-resolution scanning electron microscope operating at 20 KV. Micrographs were taken at variable magnifications up to 10,000X. Similar steps or magnifications were duplicated for each specimen. A digital data keyboard entry system was used to incorporate a permanent record on each micrograph. This record included the KV, magnification, micron bar, plate number, laboratory location, and specimen code number which was assigned to each plerocercoid.

Eight longnose suckers collected with the cutthroat trout were examined for parasites using the same methods of study.

RESULTS AND DISCUSSION

The results for the 1985 parasite survey for *Salmo clarki* found in Yellowstone Lake are listed in Tables 1 and 2. The cutthroat trout ranged in total length from 200 to 400 mm and weighed from 250 to 525 grams.

In comparison with the previous survey (Heckmann 1971), three protozoan species and the spiny-headed worm, *Neoechinorhynchus rutili*, were not observed. These parasites were rarely present during the 1971 survey in which 250 fish were checked for parasites from 34 collection sites. Four parasites were added to the current list (Table 3) following the 1985 survey.

Cutthroat trout had at least six different species of parasites that included both protozoa and helminths (Table 3). The greatest number of different parasite species per fish observed was nine. Each parasite will be discussed separately and compared with a checklist of parasites for cutthroat trout in North America. One limitation of this study was the number of fish sampled representing only two sites on Yellowstone Lake.

For the eight longnose suckers, *Catostomus catostomus*, there were only three parasites observed (Table 4). These parasites are included in the discussion of cutthroat trout parasites.

Trichophrya

Trichophrya is a genus of suctorian ciliate that commonly infests the gill surface of fishes throughout the world. Their usual mode of reproduction is by endogenous buds.

Trichophrya clarki (Figs. 1a, 1b) (Heckmann 1970, Heckmann and Carroll 1985) was found on the gills of all cutthroat trout examined from two sites on Yellowstone Lake, Yellowstone National Park, Wyoming, during the summer of 1985. *Trichophrya catostomi* (Heckmann 1970, 1971) was present on the gills of 100% of the adult longnose suckers examined from the same region (Tables 1, 4).

Butschli (1889) reported *Trichophrya* in perch (*Perca*) and pike (*Esox*) from Europe and assigned the species name *T. piscium*. Davis (1937, 1942) was the first to report *Trichophrya* in the northern hemisphere. He assigned the names *T. micropteri* and *T. ictaluri* for the gill parasites of smallmouth black bass (*Micropterus dolomieui*) and channel catfish (*Ictalurus punctatus*), respectively. No name was given for *Trichophrya* in brook trout (*Salvelinus fontinalis*). He also was the first to suggest that it may have a pathogenic effect. Culbertson and Hull (1962) summarized all host records of *Trichophrya* and suggested *T. piscium* be used for all species found in fishes. This suggestion was followed by Sandeman and Pippy (1967), who reported on four salmonids of Newfoundland infested with *Trichophrya*. Hoffman (1967) stressed the need for further taxonomic study of trichophryan species and their symbiotic effects.

For our study, light microscopy disclosed extensive pathology and an average of 7.1% of the gill epithelium covered for longnose suckers due to *T. catostomi*. However, no damage was observed at the light level of magnification for *T. clarki* in cutthroat trout that had an equal area of the gill covered.

Electron micrographs (Heckmann and Carroll 1985) show damage to immediate host gill cells by both parasites, depicted by a reduction and lack of mitochondria. Both parasites form attachment helices (0.52 x 0.04 μm), which function for maintenance of parasite position on the host cell. Protozoan feeding on host tissue may be accomplished by use of necrotic gill tissue and mucus (Heckmann and Carroll 1985).

Myxosoma

During the 1985 survey one cutthroat trout had white cysts in the gills and skin that contained spores of a *Myxosoma* sp. Heckmann (1971) reported the presence of another myxosporean in the same sites.

Myxosporeans are diagnosed when the parasite is in the spore stage; opaque white cysts containing spores are visible on the fish. Histozoic species, such as those of *Myxosoma*, usually form large cysts that can be seen without magnification. The identification of the myxosporean is customarily based on the spore morphology. Each spore contains a single sporoplasm and one to four polar capsules with coiled filaments (Hoffman 1967).

The life cycle is direct, from fish to fish. This has been experimentally verified for *Myxidium*, *Chloromyxum*, and *Leptotheca*, but not for other genera. After ingestion, the sporoplasm leaves the spore, presumably penetrates the intestine, and migrates to the final site, which is often very specific for a given species. The sporoplasm grows into a trophozoite, the nuclei divide, and the structure usually grows to produce many spores in a cyst or in a single trophozoite. If the cyst is near the surface, it may rupture and the spores will

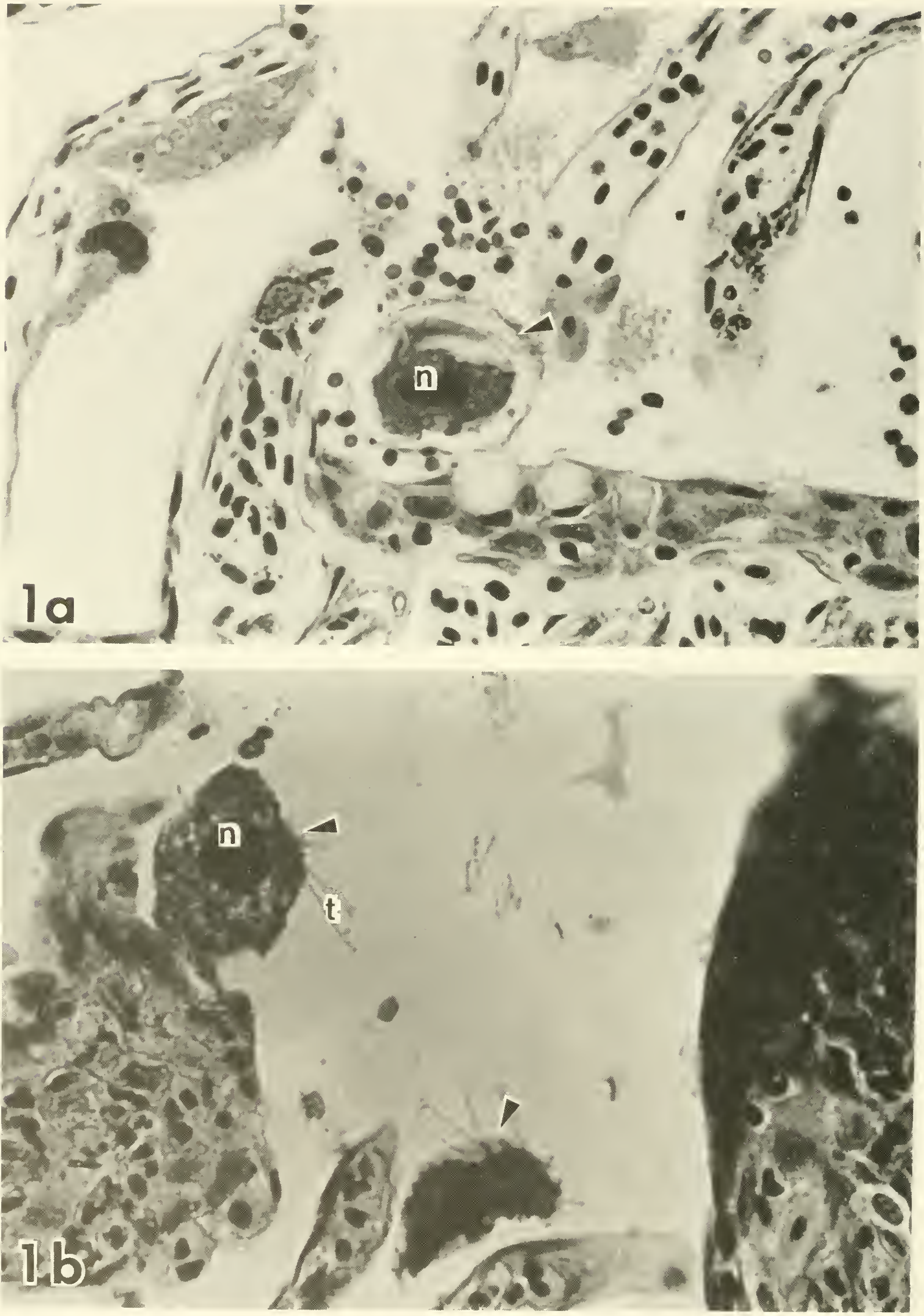

Fig. 1a, 1b. *Trichophrya clarki* (arrows) infesting the gills of *Salmo clarki*. Note the large macronucleus (n) and tentacles (t) characteristic of suctorian ciliates (400X).

be freed in the water. If the cysts are internal, the fish must die and disintegrate to free the spores (Hoffman 1967).

Myxosoma is characterized by an oval spore with two piriform polar capsules at the anterior end. The sporoplasm of the trophozoite does not contain an iodinophilous vacuole. Most of the known species are histozoic (Hoff-

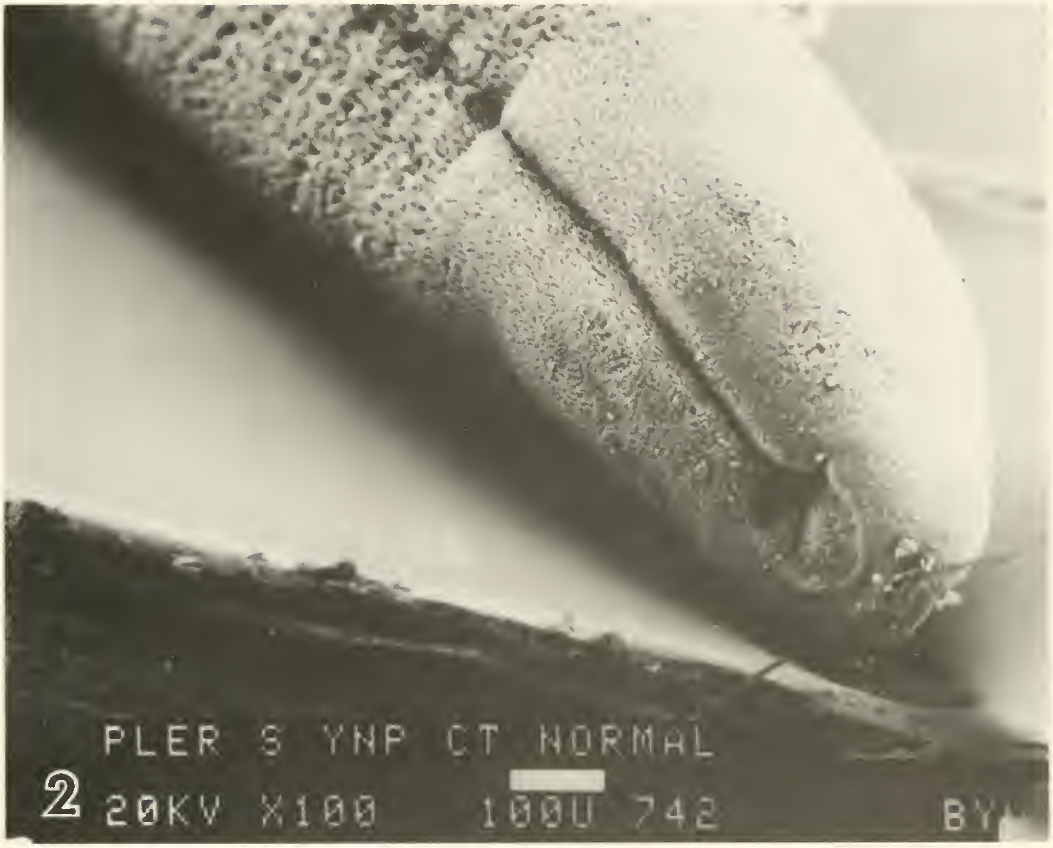

Fig. 2. Scanning electron micrograph of the anterior end of the plerocercoid stage of *Diphyllobothrium ditreum* found in *Salmo clarki* (100X).

man 1967, Hoffman et al. 1965).

Diphyllobothrium

The plerocercoid stages of *Diphyllobothrium* parasitize salmonid fishes of Yellowstone Lake, Wyoming, and other lakes in Yellowstone National Park. The parasites are found primarily in the cutthroat trout of Yellowstone Lake. *Diphyllobothrium* plerocercoids have been known in fishes of Yellowstone National Park since the first formal publication by Leidy (1872). Linton (1891b) gave the first description of adult cestodes taken from pelicans from the lake area.

In the current study, plerocercoids of *Diphyllobothrium* were present in all cutthroat trout examined from two locations on Yellowstone Lake.

Much confusion has evolved on the taxonomic relationship of *Diphyllobothrium* species (Otto and Heckmann 1984). In our study, two species of *Diphyllobothrium* plerocercoids were found: *D. ditremum* (Fig. 2) and *D. dendriticum* (Fig. 3), based on identifications by Ching and Andersen (personal communication) and Andersen (1977).

The life cycle of *Diphyllobothrium* species in Yellowstone cutthroat trout would be similar to the life cycles of other *Diphyllobothrium* species. A typical life cycle would be as follows: the egg, upon being deposited in the water, develops and hatches into a ciliated coracidium. The coracidium is then eaten by a crustacean host where it passes through the stomach wall and encysts in the tissues of the body cavity. The procercoid then develops within the crustacean. It remains within this host until the crustacean is eaten by a trout or other fish. The procercoid is then released upon ingestion and digestion of the crustacean. It migrates through the wall of the alimentary tract of the fish and develops into a plerocercoid.

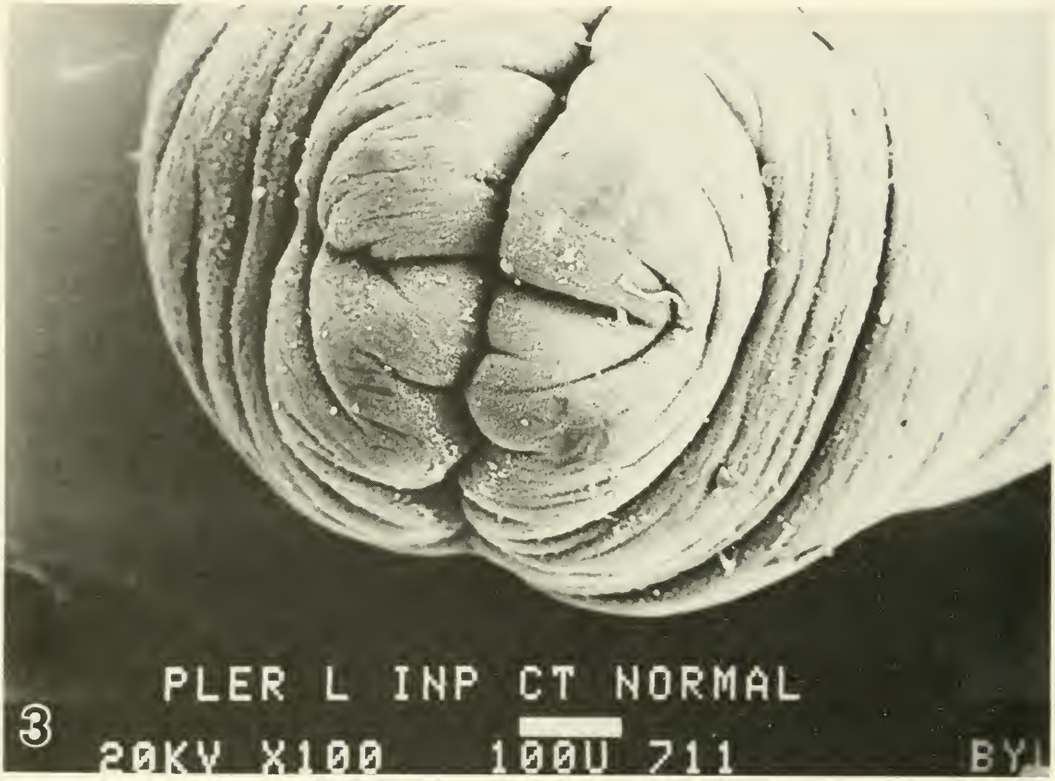

Fig. 3. Scanning electron micrograph of anterior end of the plerocercoid stage of *Diphyllobothrium dendriticum* found in *Salmo clarki* (100X).

The organism encysts in the cecal wall, mesentery, or other abdominal organs. The plerocercoid continues to grow until it can break from the cyst and become free in the abdominal cavity of the fish. The plerocercoid may then migrate into the flesh and become encapsulated. Instances of plerocercoids entering the muscle have been found where part of the plerocercoid remains in the body cavity and part is in the muscle. Plerocercoids are never encysted if they are in the body cavity or in the muscle tissue.

Plerocercoids of *Diphyllobothrium* are released from cysts or from muscle tissue of the fish when they are taken as food by the primary host. The plerocercoid then develops into an adult cestode within the intestine of the primary host which is multiple for cutthroat trout.

The primary hosts for the adult *Diphyllobothrium* in Yellowstone Lake are white pelicans (*Pelicanus erythrorhynchus*), California gulls (*Larus californicus*), and American mergansers (*Mergus merganser americanus*) (Otto and Heckmann 1984).

The definitive hosts feed on infected fishes containing the plerocercoids. Information on man as a definitive host for *Diphyllobothrium* continues to be published (Arh 1960, Margolis et al. 1973, Ohbayashi et al. 1977). Woodbury (1932) ingested eight small plerocercoids, some free and some encapsulated, in late summer of 1931. Fecal examinations were made through November, after which an antihelmintic was taken in December. No evidence of infection was found. The experiment was repeated the next year. Six larger plerocercoids (20–70 mm in length) were ingested. Fecal examinations for *Diphyllobothrium* eggs were negative. Scott ingested plerocercoids from Yellowstone Lake trout at various times with negative results (Post 1971). However, Vik (personal communication 1985) ingested plerocercoids and passed adult worms, indicating that human infections are possible. Crosby (1970) found that plerocercoids from Yellowstone Lake cutthroat trout resulted in viable, egg-producing adults in experimentally fed dogs.

The physiological effect of the plerocer-

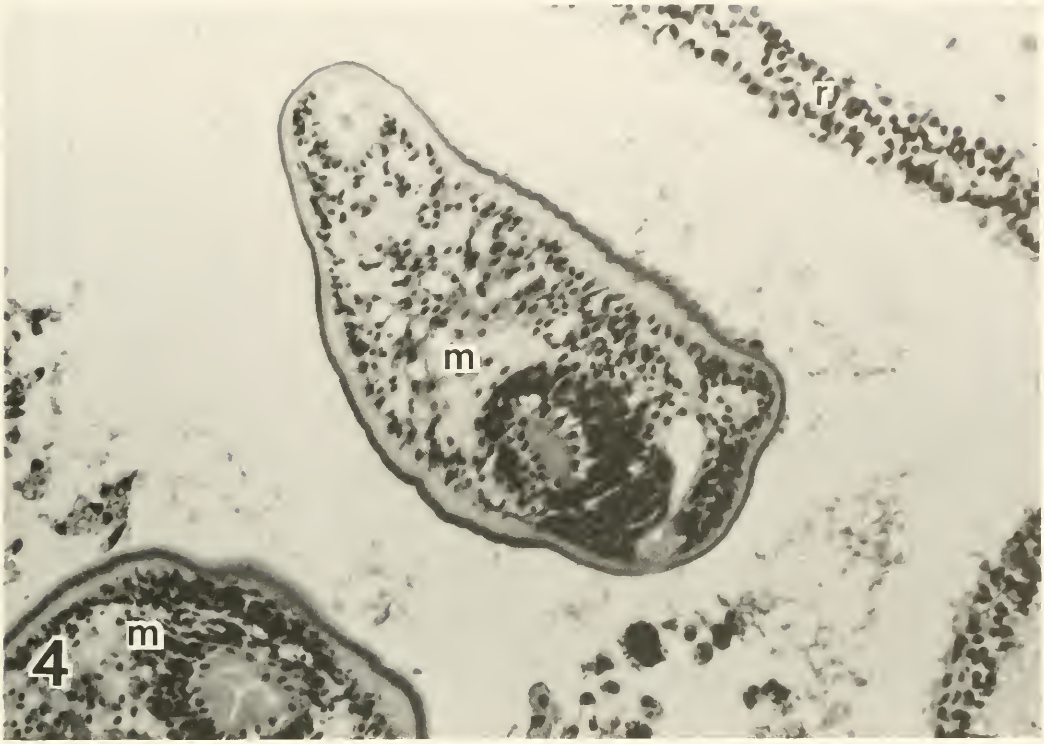

Fig. 4. *Diplostomum baeri*, metacercariae (m) found in the retina (r) of *Salmo clarki* (400X).

coids in the fish intermediate host were referred to by Linton (1891a). These fish were described as being "emaciated." Other authors stressed this point, and today one may see such fish within the park. Heckmann (1971) noted that one fish taken from the west side of Yellowstone Lake near West Thumb had more than 400 plerocercoids.

Nothing has been done to assess the effect of sublethal infections of this parasite on the fish from Yellowstone National Park, and quite heavy loads of plerocercoids may be carried by young, vigorous fish without harm. However, moderate loads of plerocercoids may be reducing the vitality of even the most vigorous fish (Post 1971).

Recently, Otto and Heckmann (1984) studied the histopathological effects of the plerocercoids on host fish in Yellowstone Lake. Eight cutthroat trout from the Yellowstone River and Yellowstone Lake were examined by histological technique and scanning electron microscopy to determine the response of host tissue to the presence of diphyllobothriid larvae. Intact plerocercoids were encapsulated with connective tissue that was infiltrated with lymphocytes and macrophages. Granulomatous tissue that was fibrotic was also present. Pancreatic tissue was displaced in infections associated with the alimentary tract. The liver showed general necrosis with edema, and the spleen demonstrated a reduction in cellularity and increased connective tissue. Testicular tissue compressed by an adjacent plerocercoid appeared to be in an otherwise normal stage of development. Necrotic myofibrils near encapsulated parasites were separated by edema and fatty infiltration. In general, *Diphyllobothrium cordiceps* did not appear to produce a serious debilitation of cutthroat trout (Otto and Heckmann 1984).

Diplostomum: Metacercariae, Flukes

Diplostomum baeri bucculentum (Fig. 4) and *D. spathaceum* (Fig. 5) are strigeid trematodes (Diplostomatidae) with a metacercarial stage that causes a disease known as diplostomatosis or eye fluke disease of fishes (Doss et al. 1963). Because of the circumglobal nature of diplostomatosis as well as the severe

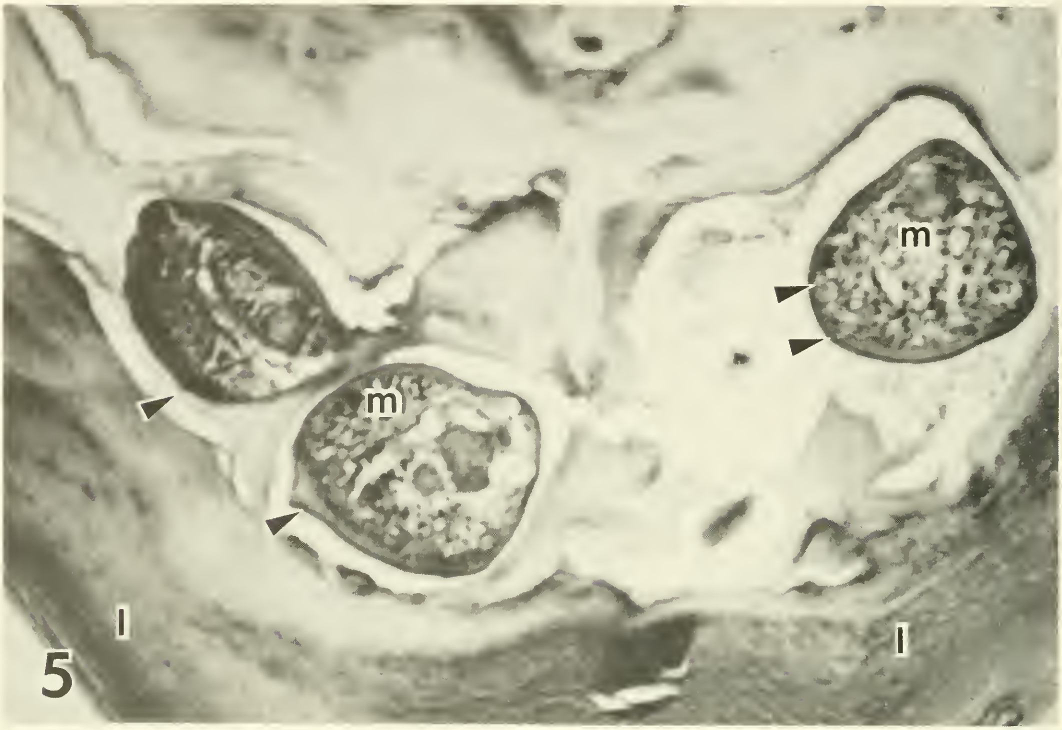

Fig. 5. *Diplostomum spathaceum*, metacercariae (m) found in the lens (l) of *Catostomus catostomus* (400X).

effects upon fish, amphibian, reptilian, bird, and mammalian lenses, much literature relating to this trematode exists. Cutthroat trout from Yellowstone Lake had a 100% incidence of *D. baeri*, with some fish containing over 100 metacercariae per eye (Table 1).

Fish are the most common second intermediate hosts for *Diplostomum;* however, infections in amphibians, reptiles, and mammals have also been reported (Ferguson 1943). Once the cercariae have penetrated the second intermediate host, they lose their forked tails and migrate to the tissues of the eye where the metacercariae develop in 50–60 days (Erasmus 1958). Diplostomatosis can cause cataracts of the lens tissue, due to the presence of the metacercarial stage of this parasite. Visual acuity for infected fish can be slightly hampered or lost, depending on the number of worms present. In addition to visual loss, fish show retarded growth and a change in food habits. In older fish, chronic infections produced subacute inflammatory reactions in the vitreous involving heterophils and eosinophils, and macrophages with ingested lens material have been observed (Dollfuss 1949, Heckmann 1983, Palmeiri et al. 1976).

There are many possible techniques to pursue concerning the control of diplostomatosis. One that shows promise is biological control by the use of a hyperparasite, *Nosema strigeoidea* (Microspora). Hussey (1971) reported the above species to be host specific for hyperparasitizing sporocysts of *Diplostomum spathaceum.* Palmieri and Heckmann (1976) and Palmieri et al. (1976) substantiated Hussey's work for eye fluke infections of fish in Utah.

Reviews of the complete life history for *Diplostomum spathaceum* and *D. baeri* are found in Palmieri et al. (1976), Ching (1985), Davies (1972), and Hoffman and Hundley (1957).

The pathological effects of *Diplostomum* metacercariae upon the fish host are many. Examination of those fish blinded with cataract and containing a heavy burden of larval metacercariae revealed stunted growth (length, girth, and weight), abnormal feeding behavior (lack of response to visual stimuli), and decreased vital acuity (Palmieri et al.

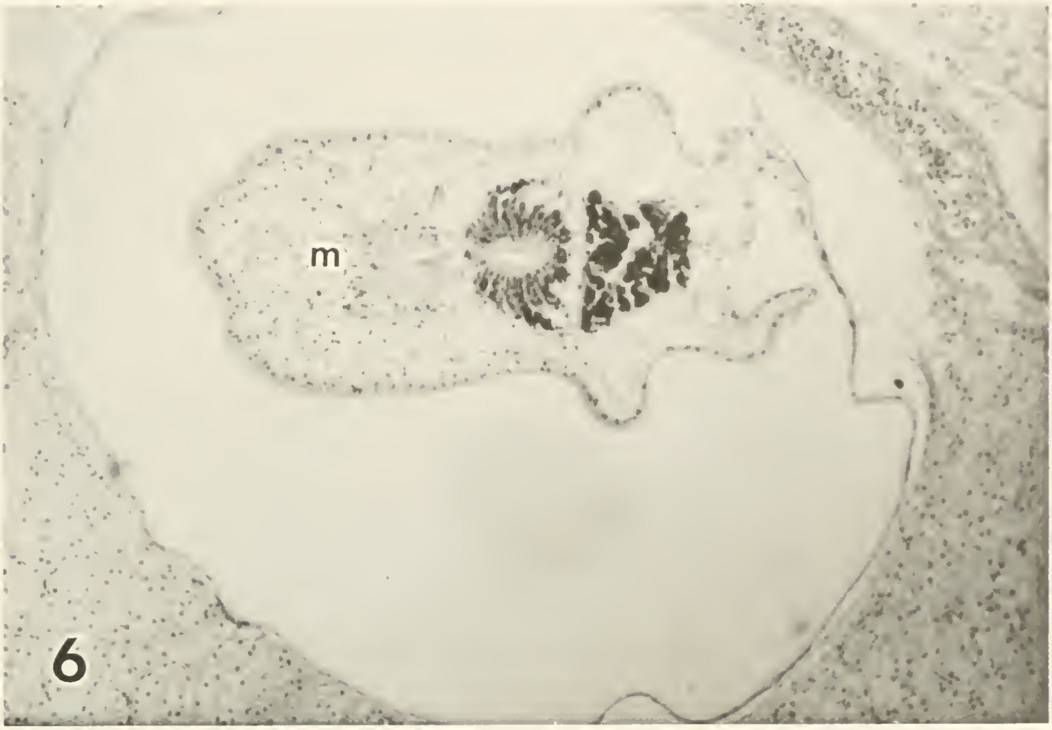

Fig. 6. *Posthodiplostomum minimum*, metacercariae (m) found in the viscera of *Salmo clarki* (400X).

1976, Heckmann and Palmieri 1978). Ashton et al. (1969) reported that larvae migrate to the eye via vascular-venous channels; he demonstrated that the lens, vitreous, or cortex of the eye may be substantially damaged. Ferguson (1943) reported that metacercariae could develop in the lens of a variety of experimentally infected vertebrate hosts including mammals. Thus, there is a potential human hazard for these parasites (Ashton et al. 1969).

Ching (1985) clarified the differences between the metacercariae of the two species of *Diplostomum* reported for this study.

Posthodiplostomum

The metacercariae were found in the viscera of only 8% of the examined cutthroat trout, *Salmo clarki*. An excellent review for this common fish parasite is found in Spall and Summerfelt (1969a, 1969b). Metacercariae have been found in all visceral organs but occur in abundance in the liver, spleen, kidneys, mesenteries, sinus venosus, heart, and ovaries. Avault and Allison (1965) found that the heart, liver, and kidneys contained approximately 79% of the total metacercariae in bluegill (*Lepomis macrochirus*).

Early literature concerning the classification of *Posthodiplostomum minimum* (Fig. 6) has been reviewed by Miller (1954), Hoffman (1958), Bedinger and Meade (1957), and Spall and Summerfelt (1969b).

Metacercariae of the strigeid fluke, *Posthodiplostomum minimum*, the white grub, are reported in many American helminthological surveys of fishes. The metacercariae, first reported over a century ago, occur in abundance in many of the 100 species of North American fishes (Hoffman 1967). They are generally so numerous in the liver, kidney, heart, and other viscera that many observers have considered them to be histopathogenic. The pathogenicity of the larval stage is usually due to compression or occlusion of the vital organ.

The occurrence of numerous metacercariae in visceral organs suggests deleterious effects on the well-being of the host and implicates *Posthodiplostomum minimum* as a cause of mortality or morbidity to its host. Hunter (1937, 1940) stated that death resulted if sufficient liver or other visceral tissue were destroyed by the metacercariae. Wild fish, with several hundreds of encysted metacercariae in the liver, sinus venosus, heart, and kidneys, are often observed to suffer no obvious debilitating effects. Colley and Olsen (1963) found as many as 991 metacercariae per bluegill with metacercariae so dense as to be clumped en masse. Spall and Summerfelt (1969a) have observed 2,041 metacercariae in a bluegill from an Oklahoma reservoir.

Mortality has been observed in the laboratory following exposure of suitable host fish to high numbers of cercariae (Hunter 1937, Bedinger and Meade 1967). Host reactions following cercarial penetration include petechial hemorrhage at the site of invasion, followed by congestion of surrounding venules, local edema, and an aggregation of leucocytes at the point of entry, particularly the phagocytic elements (Spall and Summerfelt 1969b).

Nutrition of the metacercaria involves transport across the cuticle. Oral feeding is impossible because the esophagus does not begin development until 8 days after penetration and is not well developed until 17 days; intestinal caeca develop after 17 days (Spall and Summerfelt 1969b).

After encystment (19 days), mortality infrequently occurs. There is no experimental evidence to indicate mortality or other detrimental effects from the occurrence of encysted metacercariae (Spall and Summerfelt 1969b). Compression of vital organs, such as gonadal tissue, needs to be further considered for this parasite.

Crepidostomum: Flukes, Adult Stage

In the 1985 survey all cutthroat trout were infected with *Crepidostomum farionis*. In the 1969–1970 survey, which included many more fish, 95% of the *Salmo clarki* were infected with the fluke (Heckmann 1971). The genus *Crepidostomum* is characterized by an elongated-oval to subcylindrical body. The oral suckers are terminal, surmounted anterodorsally by a half-crown, six-head papillae. The esophagus is short or moderate and the ventral sucker is in the anterior half of body. Characteristics of the life cycle are: adult in fish; oculate xiphidiocercaria in sphaerid clams; metacercaria in aquatic insects, usually mayflies, or amphipod crustaceans (Hoffman 1967).

Recent reviews of this fluke include Dollfus (1949) and Doss et al. (1964), while Amin (1982) and Hopkins (1931a, 1931b, 1934) list keys to species.

In relating the pathogenicity of *Crepidostomum farionis* to its host, Heckmann (1971) reported adult flukes in fingerling *Salmo clarki* often occupying the lumen of the gall bladder.

Bulbodacnitis: Roundworm, Nematoda

A consistent member for the parasitofauna of *Salmo clarki* from Yellowstone Lake, Wyoming, was *Bulbodacnitis*. Most adult nematodes of fish live in the intestinal tract, as is the case for this roundworm. In contrast, larval roundworms of fish may be found in almost every organ, but they are common in the mesenteries, liver, and musculature.

The life cycle of *Bulbodacnitis* always involves an invertebrate for the first intermediate host and fish, via food chains, as the definitive host. Other nematodes use the fish as the second intermediate host and develop to adults in the intestinal tract of piscivorous fish, birds, and mammals (Hoffman 1967).

Bulbodacnitis scotti was found in all of the cutthroat trout in this survey. It was one of the parasites described by Bangham (1951) in his studies of the parasites of fishes from Yellowstone Lake.

Salmincola

In the Crustacea there are two groups: the subclass Branchiura (fish lice) and the subclass Copepoda, some of which resemble free-living copepods. Certain species, such as the genera *Argulus*, *Lernaea*, and *Ergasilus*, are very serious pests in fish culture, sometimes in nature, and have become increasingly important in recent years (Hoffman 1967).

Salmincola belongs to the order Lerneopodidea, which has the following key characteristics: cephalothorax short, stout, inclined at angle to body axis; separated from trunk by groove, no distinct dorsal carapace. Trunk short and stout, often flattened dorsoventrally, with no signs of segmentation. No abdomen, caudal rami, or posterior processes. Small transparent genital process present in young females and often in adult organisms. Egg strings usually long and slender (Hoffman 1967).

They are parasitic on freshwater fishes. The typical life cycle includes the following steps:

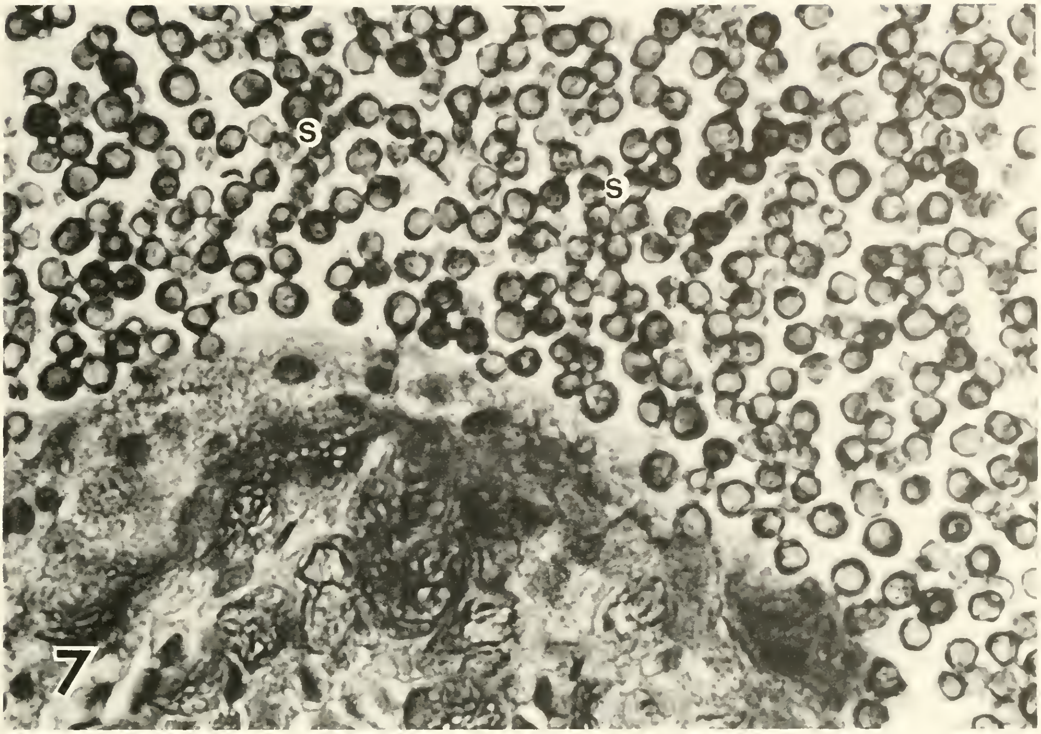

Fig. 7. Spores (s) of the fungus *Ichthyophonus* found in *Salmo clarki* (400X).

copepod hatches into small, free-swimming larva which may exist two days; larva possess mouth parts which bear a peculiar filament for attachment to fish; larva forces filament into tissue of fish and attaches second maxillae to filament which becomes the bulla, thus attaching itself permanently to fish. The entire animal undergoes degeneration, becoming a grublike parasite. The male is usually much smaller than female. Copulation occurs two and one-half to three weeks after attachment; male releases hold on gill and attaches to female. After fertilization, male dies. Each female gives rise to two batches of embryonated eggs, after which she dies. Entire life cycle takes about two and one-half months (Fasten 1912, Savage 1935, and Hoffman 1967).

Piscicola

Leeches were found on the gills and base of fins for 8% of the cutthroat trout checked during 1985 for parasites. The leeches parasitic to fish belong to the phylum Annelida. Characteristics include: mouth large, opening from behind into entire sucker cavity; fixed pharynx which is a crushing tube extending to somite XIII. Specific characteristics for *Piscicola* are: margins of body with 11 pairs of small, pulsatile vesicles, difficult to see on preserved specimens; 14 annuli per segment; body not clearly divided into anterior and posterior regions; postceca completely united into one; testisacs 6 pairs (Hoffman 1967).

Ichthyophonus, Saprolegnia

During the 1985 survey, two *Salmo clarki* had fungal infections near the dorsal fin with extensive mycelial masses penetrating the soft tissue. This appeared to be a species of *Ichthyophonus* (Fig. 7), based on current morphological characteristics.

Fungi are plantlike structures lacking chlorophyll. The assimilative phase consists of a true plasmodium or a mycelium, or rarely of separate uninuclear, independent cells not amoeboid and at no time uniting as a plasmodiumlike structure (Hoffman 1967).

Ichthyophonus, according to some sources, belongs to the Phycomycetes. Others have avoided trying to place this parasite because it is not a typical member of any class of fungi, thus referring to it as a member of the

Fungi Imperfecti.

Ichthyophonus hoferi and *Ichthyosporidium* sp. have been reported from North American rainbow trout (Erickson 1965, Gustafson and Rucker 1956, Ross and Parisot 1958). *Ichthyophonus* in rainbow trout in North America was first reported by Rucker and Gustafson (1953) from three localities in western Washington. Ross and Parisot (1958) found *Ichthyophonus* in hatcheries adjacent to the Snake River in south central Idaho.

The organism is commonly found in the kidney, spleen, liver, heart, stomach, intestine, visceral serosa, peritoneal exudate, gills, and brain. In the latest severe epizootic of rainbow trout, the spores were very numerous in the brain as well as in the musculature. Central nervous system involvement apparently resulted in partial denervation of the skeletal musculature, which caused spinal curvature. Cases have been reported on the body surface. Most of the older spores are encapsulated in small host cysts or granulomas.

The other possible taxonomic name for the fungi would be *Saprolegnia*. This is characterized by: presence of mycelium, usually continuous throughout in active assimilative phase (nonseptate). Species of the genus *Saprolegnia* are usually implicated in fungal diseases of fish and fish eggs. These fungi of fish are often considered primary or secondary invaders following tissue trauma, but once they start growing on a fish, the lesions usually continue to enlarge and may cause death to the host.

Ligula

Ligula is a common plerocercoid found in the body cavity of many species of cyprinid and catastomid fish. For the last survey conducted on the parasites of the ichthyofauna of Yellowstone Lake, two of eight longnose suckers contained *Ligula* plerocercoids. One plerocercoid measured 420 mm long by 13.5 mm wide, a length greater than that of the host. The host exhibited organ compression and atrophy, especially gonadal tissue, due to the cestode. In other cases the diseased fish show retarded growth and swollen abdomens.

Ligulosis is caused by the plerocercoid of the cestode *Ligula*, which lives in the intestine of aquatic birds, and its larvae in the visceral cavity of fish. *Ligula* has no proglot-

TABLE 5. Parasites of the cutthroat trout, *Salmo clarki*, for North America.** Those observed for *S. clarki* from Yellowstone Lake, Wyoming, are marked with an asterisk. This is primarily based on Hoffman's guide (1967) plus specific studies on Yellowstone Lake fishes. A superscript L indicates larval stage.

Protozoa:
- *Costia necatrix*
- *Ichthyophthirius multifilis*
- *Myxidium* sp.
- *Octomitus* sp.
- **Trichodina truttae*
- **Trichophrya clarki*
- **Haemogregarina* sp.
- **Costia pyriformis*
- *Myxosporidan sp.
- * *Myxosoma* sp.

Cestoda: (Tapeworms)
- *Cyathocephalus truncatus*
- *Cyathocephalus* sp.
- *^{L}*Diphyllobothrium cordiceps*
- *^{L}*Diphyllobothrium* sp.
- *^{L}*Diphyllobothrium ditremum*
- *^{L}*Diphyllobothrium dendriticum*
- *Eubothrium salvelini*
- *Proteocephalus arcticus*
- *Proteocephalus laruei*
- *Proteocephalus primaverus*
- *Proteocephalus salmonidicola*
- *Proteocephalus* sp.

Acanthocephala: (Spiny-headed worms)
- *Echinorhynchus lateralis*
- **Neoechinorhynchus rutili*
- *Neoechinorhynchus* sp.

Hirudinea: (Leeches)
- **Illinobdella* sp.
- **Piscicola salmositica*

Crustacea: (Copepods)
- *Lepeophtheirus salmonis*
- *Lernaeopoda bicauliculata*
- *Salmincola edwardsii*
- **Salmincola* sp.

Digenea: (Flukes)
- *Allocreadium lobatum*
- ^{L}*Apophallus* sp.
- *Clinostomum marginatum*
- **Crepidostomum farionis*
- *Crepidostomum transmarinum*
- *Crepidostomum* sp.
- *Deropegus aspina*
- ^{L}*Diplostomum oregonesus*
- *^{L}*Diplostomum spathaceum*
- *^{L}*Diplostomum baeri buccelentum*
- *Gyrodactylus elegans* B.
- **Nanophyetus salmincola*
- *Plagioporus siliculus*
- *Podocotyle* sp.
- *^{L}*Posthodiplostomum minimum*
- *Sanguinicola* sp.

Nematoda: (Roundworms)
- *Ascarophis globosa*
- *Bulbodacnitis globosa*

Table 5 continued.

**Bulbodacnitis scotti*
Capillaria catenata
Capillaria sp.
Contracaecum sp.
Cucullanus truttae
Cystidicola stigmatura
Cystidicoloides spp.
^{L}*Eustrongylides* sp.
Hepaticola bakeri
Metabronema salvelini
Philometra sp.
Philonema onchorhynchi
Rhabdochona cascadilla
Rahbdochona sp.

Mollusca: (Bivalves)
^{L}*Glochidia*

**Heckmann, R. A. 1971. Parasites of cutthroat trout from Yellowstone Lake, Wyoming. Prog. Fish Cult. 33: 103–106, and

Heckmann, R. A. 1985. Identification and treatment of parasites from cutthroat trout and longnose suckers, Yellowstone Lake, Yellowstone National Park. Prog. Report for YNP Service. 21 pp., and

Hoffman, G. L. 1967. Page 395 *in* Parasites of North American freshwater fishes. University of California Press, Berkeley and Los Angeles. 486 pp.

tids, and its body shows a median furrow and a fine secondary segmentation, both dorsally and ventrally. The adult lives in the intestine of aquatic birds. The coracidium escapes from the eggs deposited in the water with the excrement of the host bird. This stage is eaten by a copepod (first intermediate host) and becomes a procercoid in the abdominal cavity after having penetrated the intestinal wall. When an infected crustacean is eaten by a fish, the procercoid continues its growth in the abdominal cavity to become the plerocercoid stage, which is present in the longnose suckers.

Histopathologically it is possible to demonstrate compression atrophy, local necrosis, and hemosiderin deposits in the periphery of the liver due to *Ligula* (Pitt and Grundman 1957).

The results of this study are compared with the 1971 survey (Heckmann 1971) and with the known parasites for cutthroat trout for North America (Table 5). Much data exist pertaining to parasites of *Salmo clarki* (Hoffman 1967, Heckmann 1971), but with this brief survey four additional parasites are added to the list.

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BURROWS OF THE SAGEBRUSH VOLE (*LEMMISCUS CURTATUS*) IN SOUTHEASTERN IDAHO

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Abstract.—Burrows of the sagebrush vole (*Lemmiscus curtatus*) were analyzed by injecting them with expanding polyurethane foam. Average mean depth ± 1 SE of four burrows was 12.5 ± 2.6 cm. Tunnels were wider than high and flat on the bottom. Three of four burrows were nearly linear, with an average of five entrances. Burrows usually contained one nest made of *Artemisia tridentata* bark. No middens or communal nests were found. The burrow structure in sagebrush habitat suggests that sagebrush voles occur singly or in pairs rather than in colonies.

The sagebrush vole (*Lemmiscus curtatus*) frequently has been described as a colonial species, and clusters of their burrows have been referred to as colonies (Hall 1928, 1946, Soper 1931, James and Booth 1952, Maser et al. 1974). A few investigators have described the structure of sagebrush vole burrows (Johnson et al. 1948, Dearden 1969, Maser et al. 1974), but a quantitative analysis of this structure has not been published. The taiga vole (*Microtus xanthognathus*) frequently has underground structures such as middens and large winter nests which reflect their social organization (Wolff and Lidicker 1981). In general, quantitative analyses of the burrow structure of voles are needed to elucidate the social structure of individual species as well as to determine the effects of voles on soil structure, but few investigators have done such studies.

In August 1984 four sagebrush vole burrows were injected with expanding polyurethane foam that produces an exact cast of the burrow system. The objectives of this paper are to describe the structure of sagebrush vole burrows for an Idaho population in detail and to discuss the social organization that this structure suggests.

Methods

Our population of sagebrush voles was on the Idaho National Engineering Laboratory (INEL) on a 1-ha live-trapping plot (43°31′39″N, 112°59′26″W, Butte Co., Idaho) used to analyze population trends for this species (Mullican and Keller 1986). Vegetation on the site was dominated by big sagebrush (*Artemisia tridentata*), green rabbit-brush (*Chrysothamnus viscidiflorus*), and wheatgrass (*Agropyron* sp.), which is considered typical habitat for sagebrush voles. Temperatures on the INEL range from 39 C (maximum) in the summer to −41 C (minimum) in the winter (Groves and Keller 1983). The average annual precipitation over a 30-year period prior to our study was 19.2 cm (National Oceanic and Atmospheric Administration 1984), with peak rainfall occurring in the months of May and June.

The exact location of burrows occupied by sagebrush voles was determined by tracking animals tagged with Ta^{182}. Subsequently, individuals were removed by live trapping to recover the Ta^{182} tags, and the animals were sacrificed to assess their reproductive condition (Mullican and Keller 1986). Only adult animals over 21 g existed in the burrows we examined.

In September four burrows were filled with expanding polyurethane foam with an injection system described by Felthauser and McInroy (1983). When injected, the foam hardened into an exact cast of the burrow system. The soil surrounding the cast was excavated, revealing the details of the burrow. A 1-m^2 wire grid with 10-cm^2 squares was positioned over the cast of the burrow while it was still in place, and depth below the surface was measured at 10-cm intervals along the length of the burrow. After the cast was removed from the ground, the height and width of the cast were measured at 10-cm intervals along

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TABLE 1. Depth from ground surface, height, and width of tunnels from four burrows of *Lemmiscus curtatus*. Number of measurements is in parentheses.

	Burrow			
Measurement	1	2	3	4
Depth (cm)	10.3±4.8	20.3±9.8	10.6±4.1	8.8±6.4
±1 S.D.	(n=42)	(n=6)	(n=8)	(n=15)
Width (cm)	4.8±0.6	4.5±0.6	5.2±1.1	4.6±0.5
±1 S.D.	(n=19)	(n=10)	(n=5)	(n=19)
Height (cm)	3.2±0.9	3.1±0.3	3.2±0.4	3.4±0.6
±1 S.D.	(n=19)	(n=9)	(n=5)	(n=19)

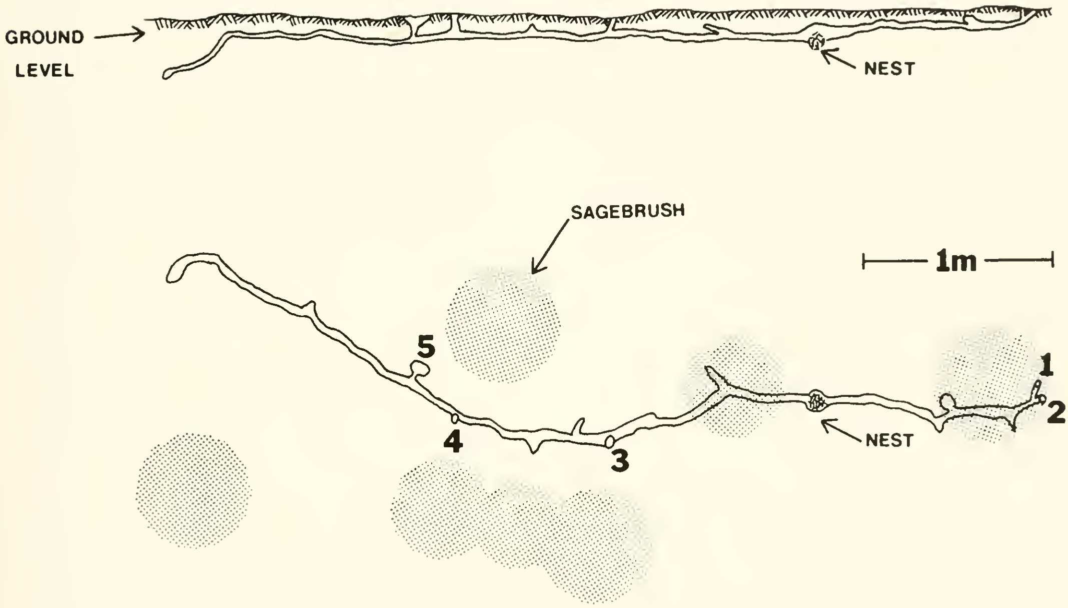

Fig. 1. Diagram of a burrow of *Lemmiscus curtatus* as determined from a polyurethane cast. Shaded areas indicate big sagebrush (*Artemisia tridentata*) canopy. Entrances are numbered.

its length. Some of the casts were incomplete because the pressure of our injection system was insufficient to completely fill the tunnels. Because of this, we could not obtain measurements of the height and width of the tunnels along some sections of the burrows. Position and number of entrances, nests, and nest chambers were readily apparent from the cast.

RESULTS

The average mean depth ± 1 SE of the four burrows was 12.5 ± 2.6 cm. Mean depths ± 1 SD of individual burrows ranged from 8.8 ± 6.4 cm to 20.3 ± 9.8 cm (Table 1). The burrow entrances were usually under or near big sagebrush (*Artemisia tridentata*), and often tunnels were found between adjacent sagebrush (Fig. 1). The mean number of entrances per burrow system was 5 and ranged from 2 to 7. The burrow tunnels were wider than high (Table 1) and were usually flat on the bottom.

Three of the burrows were nearly linear, but one was complicated in structure with tunnels radiating outward from a central nest chamber. Maximum straight-line length of burrows ranged from 0.7 to 4.6 m with a mean of 1.9 m.

Three of the four burrows contained nests that averaged 12.4 cm in diameter. Two of the nests were composed entirely of shredded sagebrush bark, whereas one occupied by a male was composed mostly of the bedding material used in the live traps and a small amount of sagebrush bark. No young were found trapped in any of the nests.

DISCUSSION

The burrows that we examined were much less extensive than those reported by Maser et al. (1974), who described a burrow system that covered an 11 x 26 m area. However, the burrow systems described by Maser et al. (1974) proved to be abandoned burrows of the northern pocket gopher (*Thomomys talpoides*) taken over and modified by sagebrush voles. Although there is no way to know if the burrows that we described were constructed exclusively by sagebrush voles, the size of the tunnel precludes previous development by pocket gophers on our study plot.

We found that the average depth of burrows was 12.5 cm. Johnson et al. (1948) found that burrows ranged from 10 to 30 cm below the surface. Dearden (1969) found that sagebrush vole burrows were shallow, extending to an average depth of 36 cm. Maser et al. (1974) stated that pocket gopher burrows invaded by sagebrush voles were usually 5 to 8 cm below the surface.

Burrows of the taiga vole, *Microtus xanthognathus*, are limited to the upper 15 to 25 cm of the soil due to mineral soil or permafrost (Wolff and Lidicker 1980). Apparently taiga voles must resort to group nesting to conserve energy during the long winter period (Wolff and Lidicker 1981). At least six other rodent species are known to nest in groups (West and Dublin 1984). We found no evidence of coloniality in the sagebrush vole, but sagebrush voles may employ communal nesting during winter, especially if snow cover is limited. However, the density of vegetation in sagebrush-grassland areas in Idaho may not be adequate to support large concentrations of these voles. Because we did not inject burrows during winter, our burrow structures would not reflect potential seasonal changes in the social organization of sagebrush voles in winter. Studies are needed to understand how this species can conserve enough energy to survive and produce offspring during winter, as we initially experienced difficulty keeping individual animals alive if they were held in live traps for more than four hours.

Sagebrush vole burrows have been reported to have up to 30 entrances (Hall 1946, James and Booth 1952). The four burrows that we excavated contained an average of 5 entrances (range 2–7). The higher number of burrow entrances reported in other studies could be due to other species that previously occupied the burrow, the fossorial work of other species which share the burrows of *Lemmiscus* (Miller 1930), or incorrect assumptions about the below-ground structure of burrows that were not excavated by investigators.

Soper (1931) found that sagebrush voles in southern Alberta and Saskatchewan constructed extensive runways between burrows. He located sagebrush vole burrows by capturing individuals in traps placed in runways near burrow entrances. We could not find evidence of runways utilized by sagebrush voles on our study plots, as most of the ground surface on this area was composed of bare soil where any trail would be quickly obliterated by frequent winds.

In areas where sagebrush (*Artemisia* sp.) is present, nests are usually made of sagebrush bark (Moore 1943, Johnson et al. 1948, James and Booth 1952). However, Maser et al. (1974) found that sagebrush vole nests were made of leaves, stems, and seed heads of grass in central Oregon.

Based on the structure of burrows, we found nothing to suggest that sagebrush voles are colonial during summer. This is consistent with the results of our dispersion analysis reported elsewhere (Mullican and Keller 1986). Further research is needed, however, during winter and at densities that exceed those we observed in Idaho to elucidate the social organization of this species.

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SPIDER FAUNA OF SELECTED WILD SUNFLOWER SPECIES SITES IN THE SOUTHWEST UNITED STATES

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Abstract.—Fifteen genera representing nine families of spiders were collected in the southwestern United States in 1980. Thomisidae, Araneidae, Dictynidae, and Saltieidae were the most commonly collected spider families. Ten genera of spiders not previously reported on sunflowers are reported for the first time.

Sunflower (*Helianthus annuus* L.) is an important oilseed crop in the United States (Cobia and Zimmer 1978). Wherever sunflower is cultivated in the United States, it suffers economic losses by insect pests (Rogers 1979). Although there are many natural enemies of sunflower pests, spiders are seldom listed among biological control agents (Rogers 1980). Cockerell (1916) reported spiders from wild *H. annuus* in California. Also, spiders were reported from cultivated sunflower in Australia (Broadley and Ironside 1981) and from commercial sunflower fields in Georgia (Lynch and Garner 1980).

Spiders prey on invertebrate pests in both natural habitats and in monotypic agricultural lands (Riechert and Lockley 1984). However, information is scant on spiders associated with wild sunflowers. Inasmuch as the encouragement and preservation of natural enemies are important factors in control of sunflower insects, we attempted to identify spiders collected from native *Helianthus* species in the southwestern United States.

Materials and Methods

Spiders were collected from native species of *Helianthus* in seven states (Arkansas, California, Colorado, New Mexico, Nevada, Oklahoma, and Texas) during September and October 1980. Spiders were hand-collected as they were encountered in pure sunflower species stands or occasionally two species stands in mid- to late-flowering growth stage. All specimens encountered were collected and preserved in vials containing 95% ethyl alcohol (ETOH). Host plant and site data were recorded for each spider specimen. The spider specimens are deposited in the museum at Midwestern State University, Wichita Falls, Texas. Spiders were identified to genus using keys in Kaston (1978). Species determinations were made using keys prepared by various authorities.

Plants were identified using the keys in Heiser et al. (1969). Specimen sheets of plants were prepared and identifications were later confirmed by C. B. Heiser, Jr. Plant specimens are deposited at the United States Department of Agriculture, Agricultural Research Service, Bushland, Texas.

Results and Discussion

In the present survey, 54 specimens of spiders were collected from 18 taxa of wild *Helianthus*. The spider collections included 9 families, 15 genera, and 7 identifiable species (Table 1). The term *identifiable* is used because some immature spiders could not be identified beyond genus. The Thomisidae (crab spiders), Salticidae (jumping spiders), Araneidae (orb-web spiders), and Dictynidae (dictynid spiders) were the most commonly collected families.

Previous reports of spiders on sunflower are from wild or cultivated *H. annuus* L. Cockerell (1916) listed *Chiracanthium inclusum* (Hentz), *Metaphidippus vitis* (Cockerell), *Tetragnatha laboriosa* Hentz, *Misumenops lepidus* (Thorell), and *Misumenoides formosipes* (Walckenaer) as being found on wild annual sunflower *H. annuus* in California. Broadley

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TABLE 1. Spiders collected from *Helianthus* species in the southwestern United States during 1980.

Family	Date of		*Helianthus* host		
Genus/species	collection	Stage	Species[1]	Location	Habitat
ANYPHAENIDAE					
Aysha sp.	Oct.	I[2]	*agrestis* Pollard (A)	CA	moist, sandy soil
ARANEIDAE					
Araneus sp.	Sept.	I	*bolanderi* A. Gray (A)	CA	steep, rocky soil
Argiope aurantia Lucas	Oct.	♀	*silphioides* Nuttall (P)	AR	shale outcrop, edge of woods
Neoscona oaxacensis (Keys.)	Sept.	♀	*petiolaris* ssp. *petiolaris* Nuttall	TX	sandy soil
Neoscona sp.	Sept.	I	*neglectus* Heiser (A)	TX	sandy soil
	Sept.	p	*niveus* (Benth.) Brandegee ssp. *canescens* (A. Gray) Heiser (A)	TX	sandy soil
CLUBIONIDAE					
Chiracanthium sp.	Sept.	I	*bolanderi* A. Gray (A)	CA	steep, rocky soil
DICTYNIDAE					
Dictyna sp.	Sept.	♀	*praecox* Englem & Gray ssp. *hirtus* Heiser (A)	TX	sandy soil
	Sept.	♀	*niveus* ssp. *canescens* (A)	NM	sandy soil
	Oct.	p	*nuttallii* ssp. *nuttallii* Torrey & Gray (P)	CO	swampy areas
	Oct.	I	*annuus* L. (A)	OK	sandy, disturbed soil
	Oct.	p	*angustifolius* L. (P)	OK	moist, edge of oak-pine woods
Mallos niveus O.P. Cambridge	Oct.	♀	*annuus* L. (A)	TX	sandy, disturbed soil
LYCOSIDAE					
Lycosa sp.	Oct.	I	*maximiliani* Schrader (P)	OK	dry loam soils
OXYOPIDAE					
Peucetia viridans (Hentz)	Sept.	♀	*debilis* ssp. *debilis* Nuttall (A)	TX	sandy soil
	Sept.	♀	*debilis* Nuttall ssp. *silvestris* Heiser (A)	TX	sandy soil
PISAURIDAE					
Pisaurina sp.	Oct.	I	*hirsutus* Raf. (P)	OK	shale outcrop
SALTICIDAE					
Icius sp.	Oct.	I	*hirsutus* Raf. (P)	OK	shale outcrop
Metaphidippus sp.	Sept.	I	*annuus* L. (A)	TX; NM	edge of cultivated field
	Oct.	I	*petiolaris* ssp. *petiolaris* Nuttall (A)	OK	sandy soil
Phidippus apacheanus Ch. & Gertsch	Sept.	♀	*annuus* L. (A)	NM; OK	disturbed area
Phidippus sp.	Oct.	I	*annuus* L. (A)	TX; OK	disturbed area
THOMISIDAE					
Misumenoides formosipes (Walck.)	Sept.	♀	*debilis* Nuttall ssp. *silvestris* Heiser (A)	TX	sandy soil
Misumenops californicus (Banks)	Sept.	♀	*annuus* L. (A)	CA	disturbed area
Misumenops sp.	Sept.	I	*praecox* Englem & Gray ssp. *hirtus* Heiser (A)	TX	sandy soil
	Sept.	I	*neglectus* Heiser (A)	TX; NM	sandy soil
	Sept.	I	*debilis* Nuttall ssp. *silvestris* Heiser (A)	TX	sandy soil
	Sept.	I	*gracilentus* A. Gray (P)	CA	steep, rocky soil
	Sept.	I	*annuus* L. (A)	NM	disturbed area
	Sept.	I	*exilis* A. Gray (A)	CA	steep, rocky soil
	Sept.	I	*deserticola* Heiser (A)	NV	sandy soil
	Oct.	I	*mollis* L. (P)	OK	sandy loam soil

[1] A annual, P perennial

[2] I immature, ♀ female, ♂ male, p penultimate

and Ironside (1981) listed *Araneus* sp., *Chiracanthium* sp., *Oxyopes* sp., and *Achaearanea* sp. as being found on cultivated sunflower in Queensland, Australia.

Spiders are conspicuous predators in cultivated sunflower. On several occasions *Misumenops* sp. immatures and adults were found feeding on larvae and adults of the sunflower moth, *Homoeosoma electellum* (Hulst), in sunflower fields of the Texas High Plains. In addition, C. E. Rogers (personal observation) has observed the green lynx spider, *Peucetia viridans*, feeding on the painted-lady butterfly, *Vanessa cardui* (L.), on *Helianthus maximiliani* Schrader in southeast Texas.

Four of the five genera reported by Cockerell (1916) were found in the present study, although not all were found on wild annual sunflower. Additionally, two of four genera found on cultivated sunflower were found on wild sunflowers. Ten genera not previously reported on sunflower are reported for the first time. These data suggest that spiders found on wild sunflowers are quite diverse; a good comprehensive list would require more concentrated sampling over longer periods of time at specific sites.

ACKNOWLEDGMENTS

We are grateful to Dr. C. B. Heiser, Jr., Department of Biology, Indiana University, Bloomington, for verifying identifications of *Helianthus* species. Travel for collecting *Helianthus* species and spider specimens was made possible by a grant from the USDA-ARS, National Plant Germplasm System, Regional Plant Introduction Station, Experiment, Georgia (Gilbert Lovell, coordinator).

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LEPTOPHLEBIIDAE OF THE SOUTHWESTERN UNITED STATES AND NORTHWESTERN MEXICO (INSECTA: EPHEMEROPTERA)

Richard K. Allen[1] and Chad M. Murvosh[2]

ABSTRACT.—Collections of mayflies of the Leptophlebiidae, genera *Choroterpes* Eaton, *Paraleptophlebia* Lestage, *Thraulodes* Ulmer, and *Traverella* Edmunds from the southwestern United States and northwestern Mexico are reviewed. *Choroterpes (Choroterpes) oaxacaensis* Brusca & Allen is synonymized with *C. (C.) inornata* Eaton. The nymph described as *Thraulodes* species "D" Allen & Brusca is the nymph of *T. arizonicus* McDunnough. New distributional records extend the known ranges of *C. inornata*, *C. (Neochoroterpes) mexicanus* Allen, *Paraleptophlebia memorialis* (Eaton), *T. arizonicus*, *T. brunneus* Koss, *T. salinus* Kilgore & Allen, *T. speciosus* Traver, *Traverella albertana* (McDunnough), and *T. castanea* Kilgore & Allen.

A study of collections of mayflies belonging to the family Leptophlebiidae from Arizona, New Mexico, and Texas in the United States and from Chihuahua, Sonora, and Sinaloa in Mexico has revealed new distribution records for species in the genera *Choroterpes* Eaton, *Paraleptophlebia* Lestage, *Thraulodes* Ulmer, and *Traverella* Edmunds. Collections by the authors are labeled by the initials C.M.M. and/or R.K.A., and their specimens have been deposited in the California Academy of Sciences, San Francisco. Specimens collected by B. C. Kondratieff and R. W. Baumann were deposited in the collection of Brigham Young University, Provo, Utah.

Genus *Choroterpes* Eaton

The subgenera *Choroterpes* and *Neochoroterpes* Allen occur in the geographic area considered by this manuscript.

Choroterpes (Choroterpes) inornata Eaton

Choroterpes inornata Eaton 1892: 6; Kilgore & Allen 1973: 321 (nymph).

Choroterpes oaxacaensis Brusca & Allen 1973: 137. NEW SYNONOMY

Brusca and Allen (1973) noted that the nymphs of *C. nervosa* Eaton and *C. inornata* were unknown and that the nymph described as *C. oaxacaensis* may eventually be found to be the nymph of the former species, as many Central American species occur in tropical Mexico. The nymph of *C. inornata* was described by Kilgore and Allen (1973) from specimens collected in Arizona and New Mexico, and a comparison of these nymphs with the type specimen of *C. oaxacaensis* reveals that they belong to a single species and therefore *C. inornata*.

DISTRIBUTION: This species is now known from southern Mexico (17° N lat.) to southern Colorado (37° N lat.).

NEW RECORDS: Arizona: Santa Cruz Co., Sycamore Canyon, 16.1 km W of Pena Blanca, 17-VIII-86, B. C. Kondratieff & R. W. Baumann. Mexico: Sonora. Rio Cuchujaqui, 16.3 km SE of Alamos, 16-I-1983, R.K.A. & C.M.M.; stream at Hacienda Cochelesi, 41.6 km SE of Aqua Prieta, 12-I-1983, R.K.A. & C.M.M.; Rio Sonora, between Uras and Mazacahui, 14-I-1983, R.K.A. & C.M.M.; stream 21.2 km N of Hwy 11 near Movas, 15-I-1983, R.K.A. & C.M.M. Sinaloa. Rio Arroyo, 53.3 km N of Elota, 14-X-1968, R.K.A.; stream 1.6 km N of El Viola, 18-I-1983, R.K.A. & C.M.M.; Rio Evora Mocorita near Mocorita on Hwy 21, 17-I-1983, R.K.A. & C.M.M. Chihuahua. Rio Pacheco, 69.4 km SW of Colonia Juarez, 27-VIII-86, B. C. Kondratieff & R. W. Baumann.

Choroterpes (Neochoroterpes) mexicanus Allen

Choroterpes (Neochoroterpes) mexicanus Allen 1974: 163.

DISTRIBUTION: This species has been reported from central Texas (32° N lat.) to Chihuahua and Veracruz, Mexico (19° N lat.).

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New records: Mexico: Chihuahua. Rio Satevo at Gral Trias on Hwy 16, 13-VIII-1977, R.K.A. Texas: Burnet County, San Gabriel River, 16-IX-1975, R. G. McClure; Uvalde County, Nueces River on Hwy 90, 6-X-1973, R. G. McClure.

Genus *Paraleptophlebia* Lestage

This genus reaches its most southern distributional limits in the southwestern United States and only *P. altana* Kilgore & Allen and *P. memorialis* (Eaton) occur in this geographic region.

Paraleptophlebia memorialis (Eaton)

Leptophlebia memorialis Eaton 1884: 98.
Paraleptophlebia memorialis, Edmunds 1962: vii; Kilgore & Allen 1973: 325 (nymph).

Distribution: This species is widely distributed in western North America from southern Alberta (53° N lat.) to Arizona and New Mexico (32° N lat.).

New records: Arizona: Apache County, stream at Greer, 27-VI-1966, R.K.A. Cochise County, Herb Martyr Lake, Chiricahua Mtns., 26-VI-1966, R.K.A. Graham County, Wet Creek at Wet Creek Canyon Camp, Pinaleno Mtns., 20-VII-1970, R.K.A.

Genus *Thraulodes* Ulmer

Allen and Brusca (1978) divided the genus into the *brunneus (brunneus, speciosus)* and the *gonzalesi (arizonicus, salinus)* groups based on nymphal characters.

Thraulodes brunneus Koss

Thraulodes brunneus Koss 1966: 91; Kilgore & Allen 1973: 325 (nymph).

Distribution: This species is known to occur from central Arizona and New Mexico (34° N lat.) to near Cabo San Lucas, Baja California, and Sinaloa, Mexico (23° N lat.).

New records: Mexico: Chihuahua. Rio Satevo at Gral Trias on Hwy 16, 3-VIII-1977, R.K.A. Rio Pacheco, 69.4 km SW of Colonia Juarez, 27-VIII-86, B. C. Kondratieff & R. W. Baumann; Arroyo Mendoza, tributary to Rio Gavilan, Gavilan Ranch, 26-VIII-86, B. C. Kondratieff & R. W. Baumann. Sonora. Rio Cuchujaqui, 16.3 km SE of Alamos, 16-I-1983, R.K.A. & C.M.M.; stream 21.2 km N of Hwy 11 near Movas, 15-I-1983, R.K.A. & C.M.M.; stream W of Locata, 23-VIII-86, B. C. Kondratieff & R. W. Baumann; Rio Maycoba, W of Maycoba, 21-VIII-86, B. C. Kondratieff & R. W. Baumann. Sinaloa. Stream 1.6 km N of El Viola, 18-I-1983, R.K.A. & C.M.M.

Thraulodes speciosus Traver

Thraulodes speciosus Traver 1934:,201; Mayo 1969: 103 (nymph).

Distribution: This species has a narrow latitudinal distribution range as it is known only from central Arizona (35° N lat.) to Chihuahua and southern Sonora, Mexico (27° N lat.).

New records: Arizona. Santa Cruz Co., Sycamore Canyon, 16.1 km W of Pena Blanca, 17-VIII-86, B. C. Kondratieff & R. W. Baumann. Mexico: Chihuahua. Rio Satevo at Gral Trias on Hwy 16, 13-VIII-1977, R.K.A. Rio Pacheco, 69.4 km SW of Colonia Juarez, 27-VIII-86, B. C. Kondratieff & R. W. Baumann; Arroyo Guacomayo, tributary to Rio Gavilan, 26-VIII-86, B. C. Kondratieff & R. W. Baumann. Sonora. Rio Cuchujaqui, 16.3 km SE of Alamos, 16-I-1983, R.K.A. & C.M.M.; stream, 21.1 km N of Hwy 11 near Movas, 15-I-1983, R.K.A. & C.M.M. Vivora Creek, 22.6 km E of Yecora, 21-VIII-86, B. C. Kondratieff & R. W. Baumann.

Thraulodes arizonicus McDunnough

Thraulodes arizonicus McDunnough 1942: 117.
Thraulodes sp. "D" Allen and Brusca 1978: 422 (nymph).

Allen and Brusca (1978) described a species of nymph collected from several localities from Honduras to Nuevo Leon and Sinaloa, Mexico, as *Thraulodes* sp. "D." The nymphal species was given an informal epithet as several Mexican and Central American *Thraulodes* were unknown in the nymphal stage. Traver and Edmunds (1967) described the male imago of *T. arizonicus* as having a distinctive black apical band on tibiae I. The tibiae of the nymphs described as *Thraulodes* sp. "D," and the tibiae of other nymphs recently collected in Arizona and in Chihuahua, Sonora, and Sinaloa, Mexico, have a black band and all are herein assigned as the nymph of *T. arizonicus*. This placement appears to be almost certain as no other *Thraulodes* species from the southwestern United States or northern Mexico is without a known nymph. A mature nymph of *T. arizonicus* is described and figured by Allen and Brusca (1978: 422).

DISTRIBUTION: This species is now known from Arizona (35° N lat.) to Honduras (14° N lat.). The very broad latitudinal distribution of this species, from the southwestern United States to tropical Mexico and Central America, is essentially the same as the distributions of *Leptohyphes ferruginus* Allen, *L. packeri* Allen, and *Choroterpes inornata*.

NEW RECORDS: Arizona. Santa Cruz Co., Sycamore Canyon, 16.1 km W of Pena Blanca, 17-VIII-86, B. C. Kondratieff & R. W. Baumann. Mexico: Chihuahua. Arroyo Guacomayo, tributary to Rio Gavilan, 26-VIII-86, B. C. Kondratieff & R. W. Baumann; Rio Pacheco, 69.4 km SW of Colonia Juarez, 27-VIII-86, B. C. Kondratieff & R. W. Baumann. Mexico: Sonora. Rio Cuchujaqui, 16.3 km SE of Alamos, 16-I-1983, R.K.A. & C.M.M; stream, 21.1 km N of Hwy 11 near Movas, 15-I-1983, R.K.A. & C.M.M. Sinaloa. Stream, 1.6 km N of El Viola, 18-I-1983, R.K.A. & C.M.M.; Rio Baluarte at Rosarito, 18-I-1983, R.K.A. & C.M.M.

Thraulodes salinus Kilgore & Allen

Thraulodes salinus Kilgore & Allen 1973: 325.

DISTRIBUTION: This species is now known from Arizona (34° N lat.) to southern Sinaloa (23° N lat.).

NEW RECORDS: Mexico: Chihuahua. Arroyo Guacomayo, tributary to Rio Gavilan, 26-VIII-86, B. C. Kondratieff & R. W. Baumann. Sonora. Rio Bavispe, 5 km SW of Colonia Moralia at dam, 12-I-1983, R.K.A. & C.M.M. Rio Maycoba, W of Maycoba, 21-VIII-86, B. C. Kondratieff & R. W. Baumann. Sinaloa. Rio Elota on Hwy 15 near Elota, 18-I-1983, R.K.A. & C.M.M; Rio Baluarte at Rosarito, 18-I-1983, R.K.A. & C.M.M.

Traverella Edmunds

Allen (1973) revised the nymphal stages of the North and Central American species, including a key to the species.

Traverella albertana (McDunnough)

Thraulus albertana McDunnough 1931: 82.
Traverella albertana Edmunds 1948: 142.

DISTRIBUTION: This species has the widest latitudinal distribution of any North American species with a range of more than 26°. Specimens have been collected from Saskatchewan, Canada (54° N lat.), to Chihuahua, Mexico (28° N lat.).

NEW RECORD: Mexico: Chihuahua. Rio San Pedro at Meoque on Hwy 45, 14-VIII-1977, R.K.A.

Traverella castanea Kilgore & Allen

Traverella castanea Kilgore & Allen 1973: 327.

DISTRIBUTION: This species is now known to occur from Arizona (35° N lat.) to Chihuahua and southern Sinaloa (23° N lat.).

NEW RECORDS: Mexico: Chihuahua. Rio Saltivo at Gral Trias on Hwy 16, 13-VIII-1977, R.K.A. Sonora. Stream 21.1 km N of Hwy 11 near Movas, 15-I-1983, R.K.A. & C.M.M.; Rio Cuchujaqui, 16.3 km SE of Alamos, 16-I-1983, R.K.A. & C.M.M. Rio Macoba, W of Macoba, 22-VIII-86, B. C. Kondratieff & R. W. Baumann. Sinaloa. Rio Baluarte at Rosario. 18-I-1983, R.K.A. & C.M.M.

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FLORA OF THE ORANGE CLIFFS OF UTAH

L. M. Shultz[1], E. E. Neely[2], and J. S. Tuhy[3]

ABSTRACT.—The vascular flora of the Orange Cliffs area, defined here as part of the Colorado Plateau floristic province, harbors approximately 209 species in 123 genera and 49 families. A species checklist is provided with a discussion of physical and floristic aspects of the region. The flora is compared statistically to the San Rafael Swell flora, which is also a subset of the Colorado Plateau. We define six vegetation types and three edaphic communities; these are described and mapped. Of eleven endemic plant species in the Orange Cliffs, three are local and rare. Sites for *Astragalus nidularius*, *A. moencoppensis*, and *Xylorhiza glabriuscula* var. *linearifolia* are discussed and mapped.

Local floras are essential for assessment of biological diversity and for making biogeographic comparisons. Unfortunately, they are available for few areas in the intermountain region. A review by Bowers (1982) shows only eight local checklists for Utah and Nevada, respectively, and most are unpublished reports. While several floras cover broader areas within the state (Arnow et al. 1980, Cronquist et al. 1972, 1977, 1984, Holmgren and Reveal 1966, Shaw 1981, Welsh 1986), the less ambitious florula, or local checklist, has the advantage of showing floristic similarities as well as discontinuities within broader floristic provinces.

Recent attention has been drawn to the Orange Cliffs area because of its unusually rich reserves of tar sands. Access is difficult and attained with a drive of over 100 kilometers on unimproved roads. Because of this inaccessibility, the area has been poorly known floristically. In 1980 we began a comprehensive inventory of the Orange Cliffs (Fig. 1) within the Glen Canyon recreational area. Our work in the area was coordinated by U.S. National Park Service personnel and was concurrent with the inventory of the Glen Canyon National Recreation Area by Welsh (1983).

The species list presented here is based on three years of field work and provides the first published checklist for the area. From an examination of herbarium records, we determined that our collections represent the first record from eastern Wayne and Garfield counties for more than 95% of the taxa listed. Additionally, we identified and described nine vegetation types for the area (Fig. 2). These include big sagebrush, blackbrush, grassland types, three pinyon-juniper associations, and three edaphically defined types designated as Chinle-shale, slope, and ephemeral wash types.

We were able to compare the flora of the Orange Cliffs area to the flora of the San Rafael Swell by using the recent publication by Harris (1983). The San Rafael Swell is a massive domal upwarp which lies northwest of the study area in Emery County and northern Wayne County. Both areas are included within the Canyonlands floristic section (Holmgren 1972). Because the two areas are in close proximity but differ in geology and topography, this study presents a special opportunity to compare two subsets of the Colorado Plateau flora, the San Rafael portion on the west and Orange Cliffs portion in the center of the Plateau.

DESCRIPTION OF STUDY AREA

Southwest of the confluence of the Green River and Colorado River, the Orange Cliffs rise above the Colorado River in a regional transition between the San Rafael Desert to the west and the Canyonlands to the east. Encompassing much of eastern Wayne and Garfield counties, the Orange Cliffs lie within the Canyonlands floristic section of the Colorado Plateau Division, a section which is the

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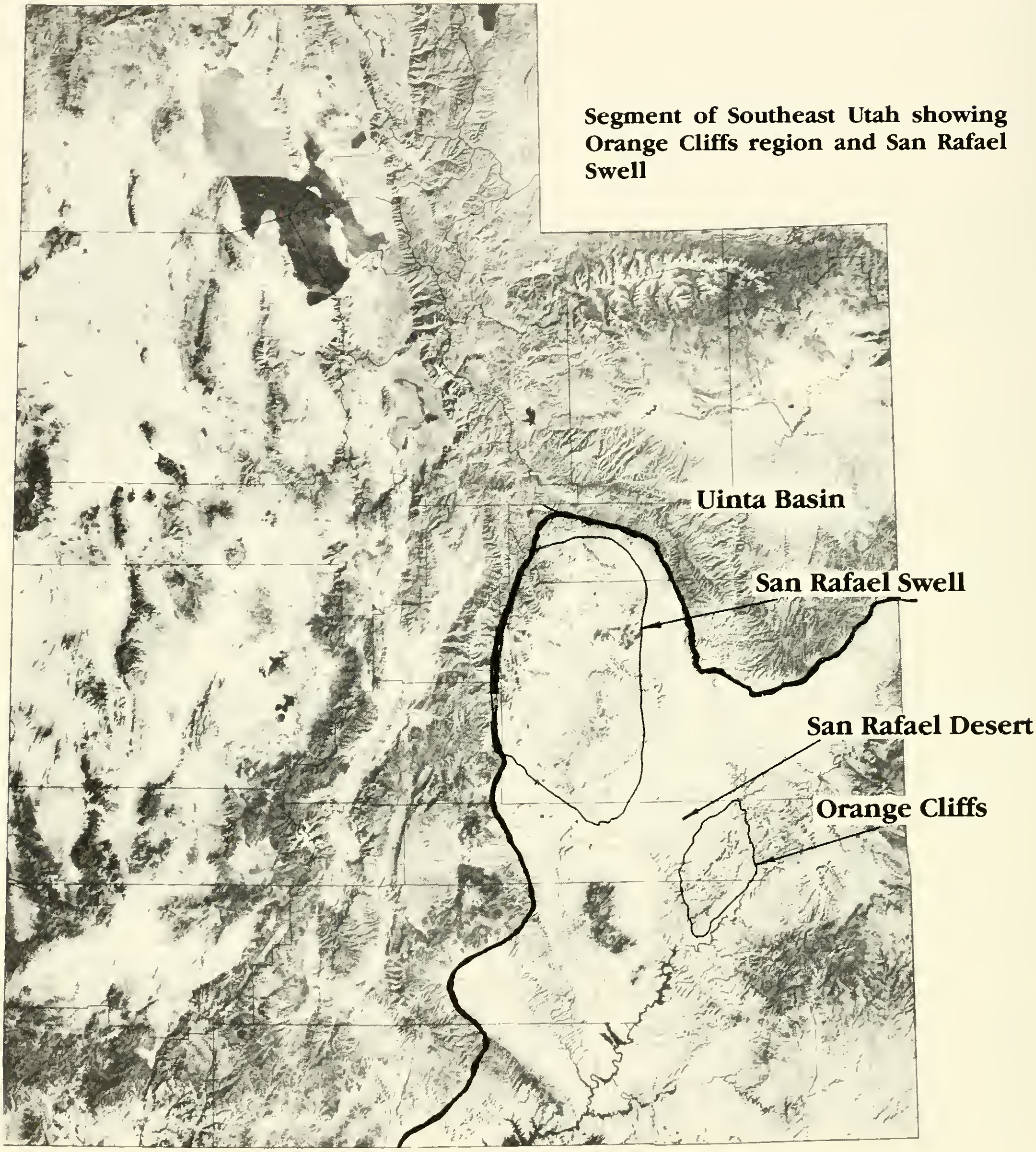
Segment of Southeast Utah showing Orange Cliffs region and San Rafael Swell
Uinta Basin
San Rafael Swell
San Rafael Desert
Orange Cliffs

Fig. 1. Map of Utah from satellite image. The Canyonlands section of southeastern Utah is roughly bounded by the dark line. The San Rafael Swell boundary encompasses the flora described by Harris (1983), with the San Rafael desert shown as an area transitional to the Orange Cliffs. (Base map reproduced by permission from Weber State College, Ogden, Utah.)

richest area for endemism in the intermountain region (Holmgren 1972).

The Orange Cliffs area lies primarily within the Glen Canyon National Recreation Area. Small portions are administered by the Bureau of Land Management or the state of Utah. The area extends from Big Ridge and Sunset Pass on the south, northward across parts of the South and Main forks of Happy Canyon (heads of tributaries of the Dirty Devil River), to French Spring on the north. The area encompasses approximately 218 km^2 (84 mi^2) with elevations ranging from 1,675 m to 2,135 m.

The Orange Cliffs region consists primarily of gently dipping sedimentary strata of Triassic and Jurassic age (Huntoon et al. 1982). The oldest rock exposed within the study area is

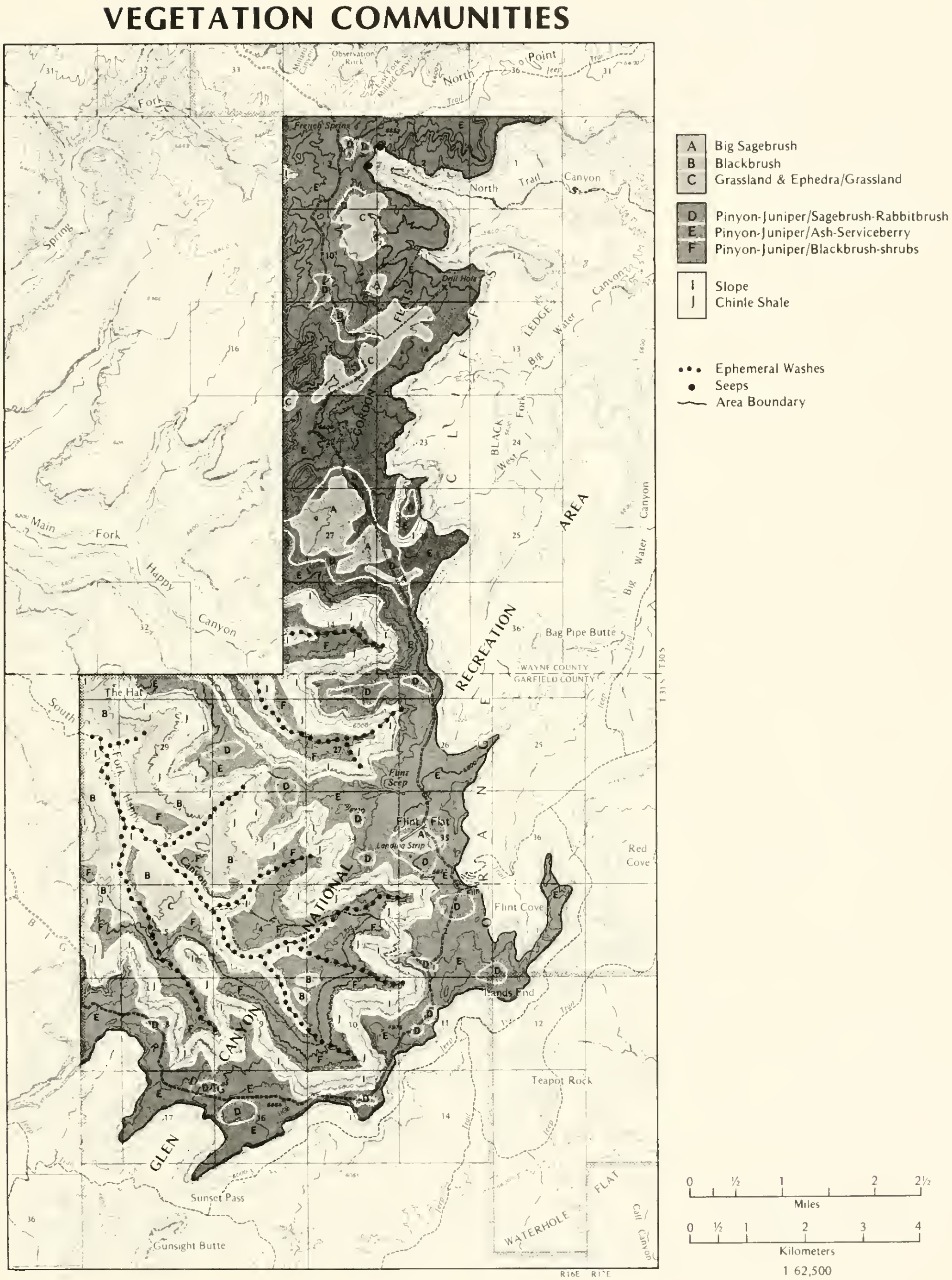
VEGETATION COMMUNITIES
A Big Sagebrush
B Blackbrush
C Grassland & Ephedra/Grassland
D Pinyon-Juniper/Sagebrush-Rabbitbrush
E Pinyon-Juniper/Ash-Serviceberry
F Pinyon-Juniper/Blackbrush-shrubs
I Slope
J Chinle Shale
Ephemeral Washes
Seeps
Area Boundary
Observation Rock
North Point
French Spring
North Trail Canyon
Drill Hole
Gordon Flats
Black Ledge
Big Water Canyon
West Fork
Main Fork
Happy Canyon
Spring
Bag Pipe Butte
WAYNE COUNTY
GARFIELD COUNTY
The Hat
South Fork Happy Canyon
Flint Seep
Flint Flat
Landing Strip
Red Cove
Flint Cove
Lands End
Teapot Rock
Glen Canyon National Recreation Area
Orange Cliffs
Sunset Pass
Gunsight Butte
Waterhole Flat
Calf Canyon
T31S T30S
R16E R17E
Miles
Kilometers
1 62,500

Fig. 2. Vegetation map of the Orange Cliffs area. Types A-F are defined by the dominant vegetation. The slope, Chinle shale, and ephemeral wash types are defined by physical factors.

the Moenkopi Formation, comprised of maroon to reddish brown sandstones, mudstones, shales, and lighter-colored carbonate layers. Above the Moenkopi is the Chinle Formation, composed of a lower sandstone and conglomerate member and an upper

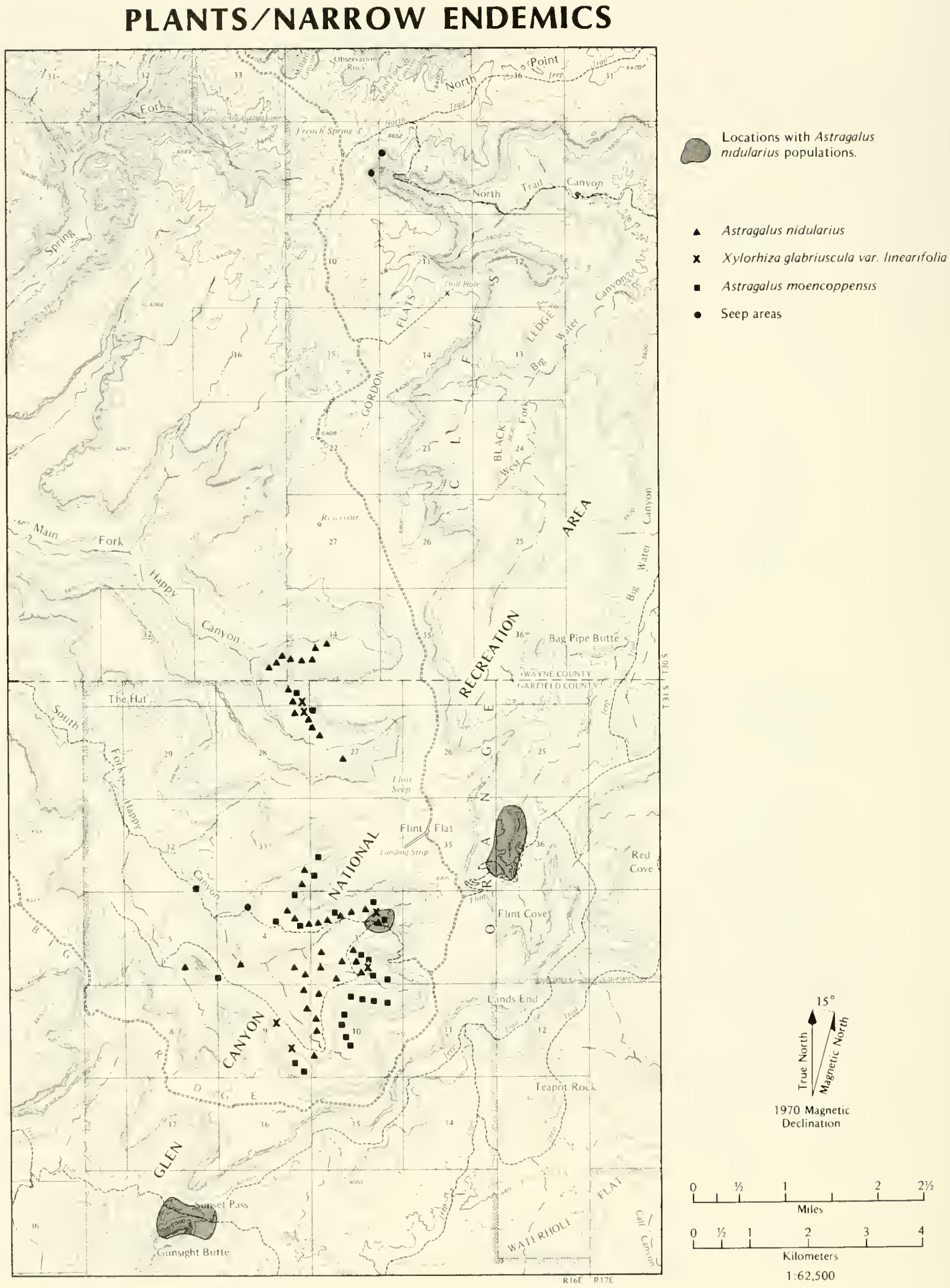
PLANTS/NARROW ENDEMICS
Locations with *Astragalus nidularius* populations.
▲ *Astragalus nidularius*
x *Xylorhiza glabriuscula var. linearifolia*
■ *Astragalus moencoppensis*
● Seep areas
ORANGE CLIFFS
GLEN CANYON NATIONAL RECREATION AREA
GORDON FLATS
BLACK LEDGE
Happy Canyon
South Fork Happy Canyon
North Trail Canyon
Big Water Canyon
Bag Pipe Butte
WAYNE COUNTY
GARFIELD COUNTY
The Hat
Flint Seep
Flint Flat
Landing Strip
Flint Cove
Red Cove
Lands End
Teapot Rock
WATERHOLE FLAT
Calf Canyon
Sunset Pass
Gunsight Butte
French Spring
Observation Rock
Millard Canyon
Drill Hole
Reservoir
Main Fork
Spring
15°
True North
Magnetic North
1970 Magnetic Declination
0 ½ 1 2 2½
Miles
0 ½ 1 2 3 4
Kilometers
1:62,500
T 30 S
T 31 S
R16E R17E

Fig. 3. Narrowly distributed soil endemics of the Orange Cliffs. Although the plant species mapped are rare, none are protected by the Endangered Species Act.

shale member. The overlying Wingate Sandstone forms the striking orange-red vertical cliffs (up to 100 m high) for which the Orange Cliffs are named. The Wingate is usually

TABLE 1. Average annual precipitation and temperatures for one station within the Orange Cliffs region (Hans Flat), one for Canyonlands (The Neck), and one for the southeast edge of the San Rafael Desert (Hanksville). Data are from NOAA (1982) and Gaylon Ashcroft, Office of the State Climatologist (personal communication).

	Rainfall (inches)	Temperature (F)		
		Maximum	Minimum	Mean
Hans Flat Ranger Station* (2,012 m elevation)	11.6		(no data available)	
The Neck** (1,808 m elevation)	9.2	63.4	41.8	52.7
Hanksville*** (1,283 m elevation)	5.2	69.4	36.7	53.1

* four-year mean (1981–84)
** twenty-year mean (1965–84)
***thirty-year mean (1951–80)

capped by the Kayenta Formation, in turn overlain by the Navajo Sandstone, which is the youngest exposed formation in the region. The Navajo is eroded from the southern part of the study area but is extensively exposed to the north on mesa tops.

The climate of the Orange Cliffs area is typical of the Colorado Plateau. Rainfall peaks are in spring, midsummer, and fall (Gaylon Ashcroft, Office of Utah State Climatologist, personal communication). Average annual precipitation and temperatures are reported for the three meteorological stations closest to the Orange Cliffs (Table 1).

METHODS

Intensive surveys were made throughout the study area over three successive field seasons from 1981 through 1983. Comprehensive collections were made of vascular plant species with voucher specimens identified and deposited in herbaria of Utah State University (UTC), Brigham Young University (BRY), and University of Colorado (COLO). Nomenclature follows Cronquist et al. (1972, 1977, 1984) and Welsh et al. (1981). Shultz, in the manuscript of Albee et al. (in press), was searched for additional reports.

The species checklist for the Orange Cliffs was compared to the San Rafael Swell flora (Harris 1983) for families, genera, species, and growth forms. We contrasted three indices of similarity, the Jaccard and Sorenson coefficients and the Otsuka Index (Simpson 1980) for comparison of the floras of the Orange Cliffs and the San Rafael Swell (based on species actually collected). The Jaccard Index measures the ratio of common to total species in two area. This was compared to the Sorenson Index, which measures the ratio of common species to the average number of species in two areas (Mueller-Dombois and Ellenberg 1974), and the Otsuka Index, whose preference is explained in a recent factor analysis (McLaughlin 1986). Formulas for similarities (S) are as follows:

$$S\,(j) = c / a + b - c \quad \text{(Jaccard Index)}$$
$$S\,(s) = c / (a + b)^2 \times .5 \quad \text{(Sorenson Index)}$$
$$S\,(o) = c / (a \times b)^{1/2} \quad \text{(Otsuka Index)}$$

where c = number of species common to both floras, a = number of species in flora one, b = number of species in flora two.

The classification of vegetation types began with a review of references dealing with vegetation types in the general area (Cronquist et al. 1972, Loope 1977). Reconnaissance on ground and by fixed-wing aircraft verified that major vegetation types of the Orange Cliffs are similar to those of Canyonlands National Park. Sites in each major vegetation type were sampled for species composition, cover, density and frequency of species; soil profiles were described on at least one site in each major type. Data are reported by Tuhy and Jensen (1983).

RESULTS

Species Numbers

We documented 209 plant species from 49 families within the Orange Cliffs area. Added to the list are 11 taxa that we expect to occur within the study area based on information in Albee et al. (in press). Of the 209 species, 12% are annuals, 62% are herbaceous perennials, and 26% are woody species. Tables 2 and 3 show the comparison of species totals and growth forms for the Orange Cliffs and the San Rafael Swell. The greatest differences are in the higher percentage of annuals in the San Rafael Swell and higher percentage of woody perennials in the Orange Cliffs. The percent-

TABLE 2. Summary of total numbers of species, genera, and families of vascular plants found in the Orange Cliffs and San Rafael Swell.

	Location	
	Orange Cliffs	San Rafael Swell
Species	209	478
Genera	123	215
Families	49	59

TABLE 3. Summary of total number (and percentage) of vascular plant species found in the Orange Cliffs and the San Rafael Swell tabulated by growth form and origin. These are compared to percentages of species compiled for all southwest floras (McLaughlin 1986).

	Orange Cliffs	San Rafael Swell	Southwest
Annuals	25 (12%)	93 (19%)	23.5%
Perennials			
Woody	53 (26%)	93 (19%)	14.2%
Herbaceous	131 (62%)	292 (62%)	58.9%
Indigenous	205 (98%)	455 (95%)	n.a.
Adventive	4 (02%)	23 (05%)	n.a.

age of adventive species is low for both areas, comprising only 2% of the species in the Orange Cliffs and 5% in the San Rafael Swell.

Endemic Plant Species

Eleven species endemic to the Canyonlands section of the Colorado Plateau were found in the Orange Cliffs area. These taxa are *Astragalus desperatus* Jones, *Astragalus moencoppensis* Jones, *Astragalus nidularius* Barneby, *Astragalus wingatanus* S. Watson, *Cryptantha osterhoutii* (Payson) Payson, *Cryptantha tenuis* (Eastw.) Payson, *Ephedra cutleri* Peebles, *Eriogonum bicolor* Jones, *Gilia subnuda* Torr. ex Gray, *Penstemon cyanocaulis* Payson, and *Xylorhiza glabriuscula* var. *linearifolia* T. J. Watson. While most of these taxa are widespread within the study area, we identified three narrowly distributed endemic plant taxa in the Orange Cliffs region which we considered sufficiently rare to warrant further investigation and precise mapping (Fig. 3). These are *Astragalus nidularius*, *Astragalus moencoppensis*, and *Xylorhiza glabriuscula* var. *linearifolia*. They are restricted to clays or sands of the Chinle Formation.

Astragalus nidularius (bird's nest milkvetch) occurs on sandy soils derived from the sandstones and conglomerates of the Chinle Formation. There are large populations of *Astragalus nidularius* in both the South and Main forks of Happy Canyon. Plants grow in little-used roadbeds and washes; typical vegetation types are pinyon-juniper and blackbrush. Populations appear healthy, as an abundance of seedlings and young plants were found in 1983.

Astragalus moencoppensis (Moenkopi milkvetch) occurs in a narrow band above the *A. nidularius* habitat in the shadscale–spineless hopsage vegetation type. It grows on the shale barrens of the upper member of the Chinle and also on the Moenkopi Formation. Most of the populations occur at the heads of both the Main and South forks of Happy Canyon.

Populations of *Xylorhiza glabriuscula* var. *linearifolia* (narrow-leaf xylorhiza) occur in the shadscale–spineless hopsage vegetation type on the upper shale member of the Chinle Formation. *Xylorhiza* occurs in association with *Astragalus moencoppensis*. Six populations were found in the Main and South forks of Happy Canyon. Populations are small in terms of both area and numbers of individuals.

Floristic Similarity

The Orange Cliffs area harbors a flora dissimilar to that of the San Rafael Swell. The San Rafael Swell is richer floristically, with a total of 478 species (Harris 1983). The Orange Cliffs region, encompassing a much smaller area (200 km^2 as opposed to 650 km^2), has a total of only 209 species (Table 2). Only 170 species are common to both regions.

The Jaccard, Sorenson, and Otsuka similarity indices, based on floristic comparison of the Orange Cliffs and the San Rafael Swell, show factors of 0.32, 0.49, and 0.56, respectively. The Jaccard Index weights the difference in total species number while the Sorenson Index averages the number of species between the two areas; both emphasize differences that are in part proportional to the inequality in sizes of the floras. The Otsuka Index minimizes the difference in size of the floras and provides an index that can be compared to other published reports for the area. The index can thus be compared to the analyses for other southwest floras published by McLaughlin (1986). The factors mapped by McLaughlin statistically define floristic provinces that have been recognized by botanists through the years. McLaughlin shows an Otsuka index of similarity of 0.70 for floras within the Canyonlands portion of southeast Utah and western Colorado, while our comparison of the San Rafael Swell and Orange Cliffs shows an index of 0.56. This is a reflection of the 39 species in the Orange Cliffs and 309 species in the San Rafael Swell that are not common to both areas. While the latter figure may be explained by greater habitat diversity in the San Rafael Swell, the number of species that do not extend from the Orange Cliffs to the Swell remains a puzzle.

Vegetation Types

Nine vegetation types were identified by dominant plant species or by topographic position. Brief descriptions of each type are presented below.

BIG SAGEBRUSH TYPE.—Big sagebrush (*Artemisia tridentata*) dominates large openings in the woodlands of the mesa tops (Gordon and Flint flats). *Bouteloua gracilis* occurs in local patches. *Bromus tectorum* and *Gutierrezia sarothrae* dominate disturbed areas. At one time these openings probably supported a much greater cover of native perennial grasses such as *Oryzopsis hymenoides* and *Stipa comata*, which are sensitive to livestock grazing (Loope 1977).

BLACKBRUSH TYPE.—Blackbrush (*Coleogyne ramosissima*) occupies benches and gently sloping flats below the cliffs of the Wingate Formation in the South Fork of Happy Canyon and large areas in the Waterhold Flat vicinity southeast of the study area. *Ephedra viridis* and *Opuntia* spp. are common associates of blackbrush in this type.

GRASSLAND TYPE.—The grassland type consists of pure grasslands and grasslands containing patches of *Ephedra cutleri*. Pure grasslands occur on deep, well-drained soils and are dominated by *Oryzopsis hymenoides*, *Hilaria jamesii*, and *Stipa comata*. They occupy small areas on flats below the cliffs of the Wingate Formation in both the Main and South forks of Happy Canyon. Associated grass species include *Sitanion hystrix*, *Sporobolus cryptandrus*, and *S. flexuosus*. Grasslands that have considerable cover of *Ephedra cutleri* are more common than pure grasslands. The subtype occurs in Gordon Flats and also occupies large areas in Waterhold Flat southeast of the study area. Species composition is very similar to that of the pure grasslands. *Gutierrezia* ssp. and *Bromus tectorum* are abundant where grazing pressure has been high.

PINYON-JUNIPER/SAGEBRUSH-RABBITBRUSH TYPE.—This type appears to be restricted to scattered locations on the mesa tops. *Artemisia tridentata*, *Artemisia nova*, and/or *Chrysothamnus viscidiflorus* occur as understory species. The soils are relatively deep.

PINYON-JUNIPER/ASH-SERVICEBERRY TYPE.—This type occupies extensive areas of the mesa tops. Common associated species include *Fraxinus anomala*, *Amelanchier utahensis*, *Cercocarpus montanus*, *C. intricatus*, and *Mahonia fremontii*. Shallow soils and slickrock outcrops are common.

PINYON-JUNIPER/BLACKBRUSH-SHRUB TYPE.—This type is almost entirely restricted to the broad, undulating benches below the cliffs of the Wingate Formation. The trees form a broken layer above scattered *Coleogyne ramosissima* and other shrubs.

SLOPE TYPE.—This type occurs on detrital rubble below the Wingate Formation that forms slopes of 35 to 80%. *Pinus edulis* and *Leymus salina* are common on these slopes and are characterized by scattered individuals of *Shepherdia rotundifolia*, *Haplopappus scopulorum*, and *Eriogonum corymbosum*.

CHINLE SHALE TYPE.—Below the cliffs of the Wingate Formation are slopes of hard-packed gray clays and shales of the upper member of the Chinle Formation. *Atriplex confertifolia* and *Grayia brandegei* are usually present on these sites. Associated species include *Atriplex canescens*, *Chrysothamnus viscidiflorus*, *Hilaria jamesii*, *Sitanion hystrix*, *Asclepias cryptoceras*, and *Hymenoxys richardsonii*.

EPHEMERAL WASH TYPE.—*Chrysothamnus nauseosus* and *Tamarix ramosissima* occur in and along ephemeral washes of the canyon bottoms in the lowest elevations of the study area. *Populus fremontii*, *Muhlenbergia asperifolia*, *Juncus balticus*, and *Hedysarum boreale* were also observed along these channels. *Rhus radicans* and *Rhamnus betulaefolia* dominate the few seep areas in the Navajo Sandstone cliffs in the northeast portion of the Orange Cliffs. *Bromus tectorum* is also present. *Adiantum capillus-veneris* occurs in smaller seep areas.

DISCUSSION

Species Richness

The Canyonlands floristic section of the Colorado Plateau harbors the richest flora of the intermountain region (Holmgren 1972). The Orange Cliffs area as a subset of Canyonlands is not particularly rich in numbers of species (209), but it does contain 11 taxa that are endemic to the Canyonlands floristic section. The San Rafael Swell (Harris 1983) is floristically richer by comparison, with 478 total species and 15 endemic species reported for the area. Eight species are strictly endemic to the Swell, whereas an additional seven species are endemic to the Swell and adjacent lands. Only one regional endemic, *Eriogonum bicolor*, occurs in both the Orange Cliffs and the San Rafael Swell.

When the Orange Cliffs and the San Rafael Swell floras are compared by the Jaccard Index (Mueller-Dombois and Ellenberg 1974), they appear to be quite dissimilar (32%). This index gives greater weight to species that are unique to either area. The Sorenson Index, which gives greater weight to species that are common to both areas, is considerably higher (49%).

Several factors may account for the somewhat depauperate flora of the Orange Cliffs area relative to the San Rafael Swell. Difference in area is important; the total area of the Orange Cliffs is approximately one-third the size of the Swell. However, the Orange Cliffs area is sufficiently large to support greater diversity. The San Rafael Swell encompasses a much wider range in elevation (1,349 to 2,500 m) than the Orange Cliffs (1,675 to 2,135 m), and geologic diversity is considerably greater in the Swell. Five geologic formations are exposed in the Orange Cliffs area while approximately 15 formations are exposed in the San Rafael Swell. Most of the rocks in the Orange Cliffs are flat-lying beds of sandstone (some shales), whereas in the San Rafael Swell there are sandstones, limestones, and shales which are tilted and exposed at all angles. Thus, the San Rafael Swell not only encompasses a larger area but also has a more diverse geology, providing potential habitat for a more diverse flora.

Grazing history may account for a decreased diversity of species in the Orange Cliffs area. There are areas, especially on the mesas, that have been subjected to a long history of grazing. The degree of grazing use is illustrated by several factors, including the presence of weedy exotics such as cheatgrass (*Bromus tectorum*), an abundance of native increasers such as matchweed (*Gutierrezia sarothrae*) and prickly pear (*Opuntia polyacantha*), and a scarcity of grass in the pinyon-juniper vegetation types. Although the area shows the effects of a long history of grazing, introduced Eurasian weeds constitute a small percentage of the flora. This may be the result of isolation from agricultural and developed areas and the relative dryness of the habitat. However, certain adventive weeds such as cheatgrass are very abundant on some sites.

Well-developed seep zones are confined to an occasional spring. Thus, the absence of hanging gardens, where there is a high concentration of endemics as well as numerous common species in southeastern Utah, would account in some measure for the depauperate nature of the flora of the Orange Cliffs. For example, *Mimulus eastwoodiae*, *Aquilegia micrantha*, *Primula specuicola*, *Carex curatorum*, and *Cirsium rydbergii*, endemics of hanging gardens found throughout Canyonlands National Park, are absent in the Orange Cliffs.

Endemism

Unusual soil types, especially those that are fine-textured, often form a habitat that harbors species specialists of narrow ecological amplitudes. As study of a species restricted to gypsum outcrops has shown (Meyer 1980), the fine-textured gypsum forms unusually dry surface layers which inhibit the seed germination of species common in coarser soils. While seeds of the soil specialists may germinate in other sites, competition from other plants substantially interferes with their growth. Thus, rare species that occur only on a particular geologic substrate are not necessarily restricted to that substrate but may be preserved from extinction by lack of competition from species less suited for that substrate (Grimes 1984). The endemics of the Orange Cliffs region are all restricted to a particular soil substrate, with those that are restricted to fine-textured clays being more narrowly restricted endemics than those found on the more common sandstone soils.

SUMMARY

With 209 species of plants, the flora of the Orange Cliffs is comparatively depauperate. The adjacent San Rafael Swell flora has more than twice the number of species. While we attribute this in part to the smaller area of the Orange Cliffs, we recognize that greater species diversity corresponds with greater geologic heterogeneity within the San Rafael Swell. The Orange Cliffs harbor fewer annuals and more species of woody perennials than the San Rafael Area. While the paucity of annuals may be due in part to isolation from well-traveled roads and management practices that have hindered the introduction of weedy annual species, the Orange Cliffs form a high plateau predominantly within a pinyon and juniper zone, a habitat that favors woody perennials. In spite of similar habitats within the San Rafael Swell, almost 20% (39 species) of the Orange Cliffs flora does not extend to the San Rafael Swell. Until we have more specific information on species distributions within the mosaic of Canyonlands habitats, however, the reasons for the relatively low similarity between two subsets of the flora must remain conjectural.

ACKNOWLEDGMENTS

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SPECIES CHECKLIST

AGAVACEAE
Yucca angustissima Engelm.
Yucca harrimaniae Trelease

AMARANTHACEAE
Amaranthus blitoides S. Wats.

ANACARDIACEAE
Rhus trilobata Nutt. in T. & G.
Rhus trilobata Nutt. in T. & G. var.

APIACEAE
Cymopterus fendleri Gray
Cymopterus purpurascens (Gray) M. E. Jones
Cymopterus purpureus S. Wats.

APOCYNACEAE
Apocynum cannabinum L.

ASCLEPIADACEAE
Asclepias cryptoceras Wats.
Asclepias latifolia (Torr.) Raf.
Asclepias macrosperma Eastw.

ASTERACEAE
Ambrosia acanthicarpa Hook.
Artemisia bigelovii Gray
Artemisia campestris L.
Artemisia dracunculus L.
Artemisia filifolia Torr.
Artemisia frigida Willd.
Artemisia ludoviciana ssp. *mexicana* (Willd.) Keck
Artemisia nova A. Nels.
Artemisia tridentata Nutt. ssp. *tridentata*
Brickellia longifolia Wats.
Brickellia microphylla (Nutt.) Gray
Brickellia oblongifolia Wats.
Chaenactis stevioides H. & A.
Chrysothamnus nauseosus (Pallas) Britt.
Chrysothamnus nauseosus (Pallas) Britt. ssp. *graveolens* (Nutt.) Piper
Chrysothamnus nauseosus (Pallas) Britt. ssp. *leiospermus* (Gray) H. & C.
Chrysothamnus pulchellus (Gray) Greene
Chrysothamnus viscidiflorus (Hook.) Nutt.
Cirsium undulatum (Gray) Spreng.
Erigeron aphanactis (Gray) Greene
Erigeron pumilus Nutt.
Erigeron utahensis Gray var. *sparsiflorus* (Eastw.) Cronq.
Gutierrezia microcephala (DC.) Gray
Gutierrezia sarothrae (Pursh) Britt. & Rusby
Haplopappus scopulorum (Jones) Blake in Tidestr.
Heterotheca villosa (Nutt.) Shinners
Hymenopappus filifolius Hook.
Hymenoxys acaulis (Pursh) Parker
Hymenoxys richardsonii (Hook.) Cockerell
Leucelene ericoides (Torr.) Greene
Machaeranthera canescens (Pursh) Gray
Machaeranthera grindelioides (Nutt.) Shinners
Machaeranthera leucanthemifolia Greene
Machaeranthera linearis Greene
Oxytenia acerosa Nutt.
Petradoria pumila (Nutt.) Greene
Senecio multilobatus T. & G.
Senecio spartioides T. & G.
Stenotus (Haplopappus) *armerioides* (Nutt.) A. Gray
Stephanomeria exigua Nutt.
Stephanomeria tenuifolia (Torr.) Hall
Townsendia annua Beaman
Townsendia incana Nutt.
Xylorhiza glabriuscula Nutt. var. *linearifolia* T. J. Watson
Xylorhiza tortifolia Greene

BERBERIDACEAE
Mahonia fremontii Fedde

BORAGINACEAE
Cryptantha confertifolia (Greene) Payson
Cryptantha crassisepala (T. & G.) Greene
Cryptantha flava (A. Nels.) Payson
Cryptantha flavoculata (A. Nels.) Payson
Cryptantha jamesii (Torr.) Payson
Cryptantha osterhoutii (Payson) Payson
Cryptantha tenuis (Eastw.) Payson
Lappula occidentalis (Wats.) Greene
Lithospermum incisum Lehm.

BRASSICACEAE
Arabis perennans Wats.
Arabis pulchra M. E. Jones var. *pallens* M. E. Jones
Caulanthus divaricatus Rollins
Descurainia pinnata (Walt.) Britt.
Draba cuneifolia R. Graham var. *cuneifolia*
Draba verna L.
Erysimum asperum (Nutt.) DC.
Lepidium montanum Nutt.
Lesquerella ludoviciana (Nutt.) S. Wats.
Physaria acutifolia Rydb.
Schoencrambe linifolia (Nutt.) Greene
Sisymbrium altissimum L.
Stanleya pinnata (Pursh) Britt.
Streptanthella longirostris (Wats.) Rydb.
Streptanthus cordatus Nutt.

CACTACEAE
Echinocereus triglochidiatus Engelm.
Opuntia phaeacantha Engelm.
Opuntia polyacantha Haw.
Sclerocactus parviflorus Clover & Jotter

CAPPARIDACEAE
Cleome lutea Hook.

CAPRIFOLIACEAE
Symphoricarpos longiflorus Gray

CARYOPHYLLACEAE
Arenaria eastwoodiae Rydb.
Paronychia sessiliflora Nutt.

CHENOPODIACEAE
Atriplex canescens (Pursh) Nutt.
Atriplex confertifolia (T. & G.) Wats.
Ceratoides lanata (Pursh) J. T. Howell
Grayia brandegei Gray
Kochia americana Wats.
Salsola paulsenii Sennen & Pau

CUPRESSACEAE
Juniperus osteosperma (Torr.) Little

ELAEAGNACEAE
Shepherdia rotundifolia Parry

EPHEDRACEAE
Ephedra cutleri Peebles
Ephedra torreyana Wats.
Ephedra viridis Cov.

EUPHORBIACEAE
Euphorbia fendleri T. & G.
Euphorbia glyptosperma Engelm.

FABACEAE
Astragalus amphioxys A. Gray var. *vespertinus* (Sheldon) M. E. Jones
Astragalus ceramicus Sheld.
Astragalus desperatus Jones
Astragalus lentiginosus Dougl. var. *palans* (M. E. Jones) M. E. Jones
Astragalus lonchocarpus Torr.
Astragalus moencoppensis M. E. Jones
Astragalus mollissimus Torr. var. *thompsonae* (Wats.) Barneby
Astragalus nidularius Barneby
Astragalus praelongus Sheld.
Astragalus wingatanus S. Wats.
Dalea flavescens (S. Wats.) Welsh
Hedysarum boreale Nutt.
Lupinus argenteus Pursh var. *argenteus*
Lupinus pusillus Pursh
Pediomelum megalantha (Woot. & Standl.) Welsh
Psalidium lanceolatum (Pursh) Welsh

FUMARIACEAE
Corydalis aurea Willd.

GENTIANACEAE
Frasera paniculata Torr. (=*Swertia utahensis* [Jones] St. John)

HYDROPHYLLACEAE
Phacelia crenulata Torr. in Wats.
Phacelia ivesiana Torr.

JUNCACEAE
Juncus balticus Willd.

LAMIACEAE
Marrubium vulgare L.

LILIACEAE
Allium nevadense Wats.
Androstephium breviflorum Wats.
Calochortus aureus Wats.
Calochortus nuttallii T. & G. in Beckwith
Zigadenus paniculatus (Nutt.) Wats.

LINACEAE
Linum aristatum Engelm.

LOASACEAE
Mentzelia albicaulis Dougl. in Hook.
Mentzelia multiflora (Nutt.) Gray

MALVACEAE
Sphaeralcea coccinea (Nutt.) Rydb.
Sphaeralcea grossulariifolia (H. & A.) Rydb.

NYCTAGINACEAE
Abronia elliptica A. Nels.
Oxybaphus linearis (Pursh) Rob.

OLEACEAE
Fraxinus anomala Torr.

ONAGRACEAE
Calylophus lavandulaefolius (T. & G.) Raven
Oenothera caespitosa Nutt. ssp. *macroglottis* Wagner & Klein
Oenothera pallida Lindl.

OROBANCHACEAE
Orobanche multiflora Nutt.

PINACEAE
Pinus edulis Engelm.

PLANTAGINACEAE
Plantago patagonica Jacq.

POACEAE
Aristida purpurea Nutt.

Bouteloua curtipendula (Michx.) Torr.
Bouteloua gracilis (H. B. K.) Lag. ex Steud.
Bromus tectorum L.
Hilaria jamesii (Torr.) Benth.
Leymus salina (Jones) A. Love
Muhlenbergia asperifolia (Nees & Mey) Parodi
Muhlenbergia pungens Thurb.
Munroa squarrosa (Nutt.) Torr.
Oryzopsis hymenoides (R. & S.) Ricker
Phragmites australis (Cav.) Trin. ex Steud.
Poa fendleriana (Steud.) Vasey
Poa secunda Presl.
Sitanion hystrix (Nutt.) J. G. Smith
Sporobolus airoides (Torr.) Torr. in Parke
Sporobolus contractus A. S. Hitchc.
Sporobolus cryptandrus (Torr.) Gray
Sporobolus flexuosus (Thurb.) Rydb.
Stipa comata Trin. & Rupr.
Stipa speciosa Trin. & Rupr.
Vulpia octoflora Walt.

POLEMONIACEAE
Gilia aggregata (Pursh) Spreng. var. *arizonica* (Greene) Fosberg
Gilia inconspicua (Smith) Sweet var. *sinuata* (Hook.) A. Gray
Gilia subnuda Torr. ex Gray
Leptodactylon pungens (Torr.) Nutt.
Leptodactylon watsonii (Gray) Rydb.
Phlox hoodii Richards
Phlox longifolia Nutt.

POLYGALACEAE
Polygala subspinosa Wats.

POLYGONACEAE
Eriogonum alatum Torr.
Eriogonum bicolor Jones
Eriogonum cernuum Nutt.
Eriogonum corymbosum Benth. in DC. var. *orbiculatum* (Stokes) Reveal & Brotherson
Eriogonum deflexum Torr. in Ives
Eriogonum inflatum Torr. & Frem.
Eriogonum microthecum Nutt.
Eriogonum wetherillii Eastw.

POLYPODIACEAE
Adiantum capillus-veneris L.

PORTULACEAE
Portulaca oleracea L.

RANUNCULACEAE
Clematis ligusticifolia Nutt. in T. & G.
Delphinium scaposum Greene

RHAMNACEAE
Ceanothus greggii Gray
Rhamnus betulaefolia Greene

ROSACEAE
Amelanchier utahensis Koehne
Cercocarpus intricatus Wats.
Cercocarpus montanus Raf.
Coleogyne ramosissima Torr.
Holodiscus dumosus (Nutt.) Heller
Purshia mexicana (D. Don.) Welsh var. *stansburyi* (Torr.) Welsh
Rosa woodsii Lindl.

SALICACEAE
Populus fremontii Wats.

SANTALACEAE
Comandra umbellata (L.) Nutt.

SCROPHULARIACEAE
Castilleja chromosa A. Nels.
Castilleja linariifolia Benth. in DC.
Castilleja scabrida Eastw.
Cordylanthus wrightii Gray in Emory
Pedicularis centranthera Gray
Penstemon barbatus (Cav.) Roth
Penstemon comarrhenus Gray
Penstemon cyanocaulis Payson
Penstemon eatonii Gray
Penstemon lentus Pennell
Penstemon palmeri Gray
Penstemon utahensis Eastw.

SOLANACEAE
Solanum triflorum Nutt.

TAMARICACEAE
Tamarix ramosissima Ledeb.

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EVALUATION OF THE IMPROVEMENT IN SENSITIVITY OF NESTED FREQUENCY PLOTS TO VEGETATIONAL CHANGE BY SUMMATION[1]

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ABSTRACT.—At four sites in Idaho, frequency was measured separately with three different-sized plots (10 x 25, 15 x 33.5, and 20 x 50 cm) arranged in a nested configuration. These individual frequency values were added together to create a summed "frequency." This summed value was compared to the original frequency values generated by each individual plot size in respect to its ability to detect range trend. The summation procedure consistently detected smaller changes in frequency than any individual plot size. In addition, the summed values detected a significant change in more species at each site. Summing the frequency values usually detected changes at a lower alpha level than did any single plot (0.10 vs. 0.20).

Range trend has historically been defined as either apparent or measured. Apparent trend is a subjective rating reached with only one observation of the land. Various site and vegetational indicators of trend are observed and judged against published standards. This approach has been described by many authors, including Pickford and Reid (1942), Costello and Turner (1944), and Ellison and Croft (1944). Measured trend is an objective record of successive condition ratings. Two or more successive observations of condition must be made over an interval of time to determine measured trend.

Before sampling for measured trend begins, the vegetational attribute with which condition (and thus measured trend) is measured must be determined. Cover, production, density, and frequency are the most common attributes considered. For management purposes, the selected attribute should exhibit the following characteristics: (1) precision, (2) ease in sampling, and (3) sensitivity to successional change. Fluctuations in any of the attributes due to between-year and between-season weather variations and current grazing use reduce the precision and sensitivity of the resulting measurements. Cover (both foliar and basal) and yield reflect these variations and, therefore, are too transient for determining trend. Density is the attribute least affected by weather variation, especially with perennial vegetation. However, as Strickler and Stearns (1963) point out, measuring density can become tedious or imprecise if the plants are small and numerous or if they reproduce vegetatively. Considering the alternatives, frequency becomes a logical choice. A search of the available literature shows various authors, including Blackman (1942), Hyder et al. (1963), and Greig-Smith (1964) alluding to the advantages of frequency for determining vegetational change. As a function of density, frequency is relatively stable over time. This stability, coupled with objective measurements, provides a high degree of precision. Brown (1954) adds that frequency is measured easily and rapidly. In addition, use of frequency as a method of monitoring range trend is becoming more prevalent (U.S. Department of Agriculture, Forest Service 1981, Despain 1982). Results presented by Smith et al. (1986) show frequency to be a sensitive measure of successional change.

Frequency, however, does have certain limitations that must be accounted for to maximize its usefulness. These limitations have been listed by Kershaw (1973) as four variables that determine frequency results: (1) plot size, (2) plant size, (3) plant distribution, and (4) plant density. A change in any one of these variables will change the resulting frequency value (Brown 1954), thus obscuring determination of the variable(s) responsible for change. It is impossible to control plant

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size, distribution, or density when sampling vegetation. Plot size, therefore, is the only variable that can be altered to give desired frequency values. Appropriate frequency values for vegetation monitoring are usually considered to be in the 63 to 86% range for the most prevalent species. At these levels, plot sizes will be one and two times, respectively, the mean area of the individuals of that species in a randomly distributed population (Curtis and McIntosh 1950).

The ideal frequency sampling scheme to account for variations in plant size, distribution, and density would include a different-sized plot for each species (Despain 1982), since a given plot size will sample certain species more adequately than others (Hyder et al. 1963). Many investigators have avoided this complexity by standardizing the plot size used on a variety of vegetation types (Shimwell 1971, Tueller et al. 1972). However, the inherent variability in plant size, distribution, and density often makes it difficult for only one plot size to adequately sample various areas.

The use of a single plot size is further constrained by Raunkiaer's Law of Frequency (Raunkiaer 1934), which states that there are more species with few individuals than with many (Shimwell 1971). This skewed distribution of frequencies can present problems in frequency sampling for range trend, since it is more difficult to detect change over time in species with low frequencies (Smith et al. 1986). Although most "key" management species monitored for range trend are not rare, there are often cases when interest is directed toward both numerous and scarce species occupying the same site. Increasing species frequency by enlarging a single plot size could improve the likelihood of detecting range trend in species having lower frequencies. However, this is not practical, since enlarging plot size would simultaneously increase frequency for all species present. If the frequency of any species reached 100%, it would become impossible to make comparisons because future increases in density of that species would still yield values of 100% frequency. Therefore, enlarging plot size could potentially narrow the range of frequency values of various species and thus reduce the total number of species having frequency values useful for determining range trend. A preferable alternative would somehow widen the range of frequencies and at the same time improve the sensitivity to change for those species with lower frequency readings.

One alternative solution might be to select one plot size, among several, best suited for a particular site. This is employed in the nested frequency plot method where three or four variously sized plots are located (nested) within each other in a single configuration. Frequencies recorded for each of the plot sizes are compared. Data from only the plot size giving the most sensitive detection of change over a period of time are used to determine range trend for a site. Although use of frequency plots has the potential to improve sensitivity for detection of trend, procedures commonly employed with the nested technique may not use data as efficiently, since data from only one of the several plot sizes are ever utilized for any given species.

This study investigated the summation of frequencies from three different nested plot sizes in an effort to increase sensitivity and efficiency for detection of trend of any individual plot size alone. For example, in 100 nested configurations each consisting of three plot sizes, a total occurrence of 300 would be possible for any given species. It is proposed that such a summation would have three advantages: (1) Compared to any single plot size, it would widen the range of possible occurrence values for any species by increasing the maximum possible number of observations from 100 to 300 (assuming three nested plots are used). Differences that might not be significant at lower frequency levels may become significant when the range of occurrences is increased. (2) The smaller plot sizes in the nested design would provide inherently smaller frequency readings. Should such smaller values be added to the total, they would decrease the probability that the summed value would reach 300. This would improve the likelihood of detecting changes in already abundant species whose frequency increased over time. (3) It should increase the number of species showing significant changes in frequency over time, adding credibility to the estimation of range trend.

METHODS

Field Methods

During the summer of 1981, four sites located within 70 km of Salmon, Idaho, were studied. These sites were selected to test the procedures in a variety of vegetational types. Listed as habitat types (Hironaka et al. 1983, Steele et al. 1981), the sites are:

1. *Pinus ponderosa/Festuca idahoensis.* Located at an elevation of 1,500 m, this site exhibited a typical fire-maintained *P. ponderosa* stand structure (Morris and Mowat 1958). It combined an unevenaged stand overstory with a grass-dominated understory.
2. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* Several *Pseudotsuga menziesii* trees had invaded this site, although there was no indication of previous occupation by this species. The elevation was 1,975 m.
3. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* This site had been burned three years prior to sampling. The elevation was 2,250 m.
4. *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis.* This site was located on an exposed, high-elevation (2,725 m) ridge. There was an abundance of small forbs and a lack of shrubs. The few *Artemisia* individuals present were small and stunted.

Vegetation data reported in this study consist of the herbaceous component only. Usage of scientific names in this report except for *Artemisia* follows that of Hitchcock and Cronquist (1973).

The sampling process consisted of three phases designed to simulate trend sampling over a period of years. In phase 1, frequency and cover baseline measurements were taken. Phase 2 consisted of randomly excluding known amounts of vegetation from further sampling, simulating a known compositional change over time. In phase 3, the plots sampled in phase 1 were resampled after the vegetation change had been created. Phases 2 and 3 were completed a total of three times, since three different levels of change were studied.

The frequency sampling unit consisted of a series of metal plot frames arranged concentrically in a nested configuration. Plot sizes were 10 x 25, 15 x 33.5, and 20 x 50 cm, representing areas of 250, 500, and 1,000 cm^2, respectively. The nested configuration allowed direct comparison of any different size, since a plant located in a particular plot would also be included in all larger plots.

At each site, ten 10-m transects were located within a uniform area. The transects were usually placed parallel to each other with a distance of 2 to 3 m between them. Along each transect, 40 of the nested configurations were uniformly spaced, for a total of 400 samples per site.

At each of the 400 nested configurations, frequency of occurrence for individual species rooted within each of the three frequency plots was recorded. These separate frequencies were also summed into one value for each species. In addition, 120 systematically located point measurements were made along each transect (1,200 points per site) to measure foliar cover. These frequency and cover measurements comprise phase 1. In phase 2, changes in density were created to simulate successional trend. To do this, randomly located sections of the transect, each 20 cm long, were established. Each section also extended perpendicularly from the transect to include all sizes of the sample plots. Any plant located within these "exclusion areas" was considered to have disappeared, thus simulating vegetation change over time. To achieve the desired levels of change (10, 20, and 30% reduction in vegetation), 5, 10, and 15 exclusion areas were located on each transect, approximating a 10, 20, and 30% reduction in ground surface area occupied by the exclusion areas. Varying amounts of change within a single sample plot were created by superimposing the randomly located exclusion areas over the uniformly spaced sample plots. It was possible for an exclusion area to fall directly on a sample plot removing all vegetation from that plot. An exclusion area could also fall between two sample plots and not affect either. However, neither of these possibilities occurred frequently. Instead, varying amounts of partial overlap occurred between the exclusion areas and the sample plots. Following each of the three levels of change, phase 3 resampled the original sample plots, minus the exclusion areas, for frequency and cover.

While this study considered "change" to be a reduction in species density, a reversal of the data could be used to illustrate the effects of species increases. With the same set of data, however, analysis of either a reduction or increase would still be possible. Since this study was testing for sensitivity to small levels of change, the amount of change induced was limited to a maximum of 30%.

The objective of this study was to compare changes in frequency levels detected by different plot sizes. Without a reference standard, it would be impossible to determine if the frequency changes detected by one plot size were more precise than any other plot size. Frequency itself could not be used as a reference for two reasons: (1) it is the value being tested, and (2) its results are highly related to plot size. For this reason, a vegetation measurement other than frequency had to be established as a reference. Density, yield, and cover were considered. For practical reasons, cover was the attribute chosen. It was found, however, that basal cover levels at the sites studied were too small to be useful. Foliar cover was thus chosen as the reference standard. It was determined that using the previously mentioned 1,200 points per site would give an accurate assessment of change. The sole purpose of the foliar cover data was to determine if a significant change had occurred as a result of the exclusion process. Normally, foliar cover is not used to determine trend; it is subject to yearly and seasonal fluctuations. However, it was used as a parameter in this study, since all sampling on a site was done within a few days' time.

Data Analysis

Sampling 400 plots is usually considered too time-consuming for most management requirements. Therefore, to test the procedure under likely operating conditions, the original 400 nested configurations were considered to be a population, from which a random sample of 200 was drawn for analysis. The 600 foliar cover points associated with these 200 samples were also used in the analysis. All results shown here are from the smaller (200 plot) sample size. Data from each of the four sites were analyzed independently; no attempt was made to combine information from different sites.

TABLE 1. Percent foliar cover before and after each exclusion level.

Exclusion level (%)	Site			
	1	2	3	4
0	20	54	45	38
10	17	50	42	34
20	15**[1]	44**	37**	31*
30	13**	39**	32**	28**

[1] * significant at α 0.20
** significant at α 0.10

Significance determined by separate t-tests between the 0% removal level and each of the "exclusion" levels within a column.

Site 1 *Pinus ponderosa/Festuca idahoensis* habitat type.
Site 2 *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type (unburned).
Site 3 *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type (burned).
Site 4 *Artemisia tridentata* subsp. *vaseyana/Festuca idahoensis* habitat type (high-elevation ridgetop).

Foliar Cover

Considering foliar cover as a continuous variable, individual t-tests were used to compare differences between control (original) conditions and each of the three "exclusion" treatments. For these tests, each of the 10 transects within a site was considered one sample. Results were compared at alpha levels of 0.10 and 0.20.

Frequency

The observations per species from the three individual plot sizes were added together to create a summed frequency value for each nested configuration. The frequency data thus contained the number of occurrences of each species per plot size (including the summed value) at the control and each "exclusion" level. For the frequency analysis, each species–plot-size combination was considered a sample. Using frequency as a discrete, present-or-absent variable, a chi-square test with Yates' correction factor (Mueller-Dombois and Ellenberg 1974) was used to determine for each plot size (including the summed value) whether significant ($\alpha = 0.20$ or 0.10) changes in frequency had occurred between the control and any of the exclusion levels. This procedure allowed for comparison of the summation results with those for each individual plot size.

RESULTS AND DISCUSSION

Foliar Cover

Results of the individual t-tests, using the foliar cover data, showed that it was not possi-

TABLE 2. Results on selected species from the Chi-square analysis on frequency for the *Pinus ponderosa/Festuca idahoensis* habitat type. The first row for each plot size contains the initial frequency and the three subsequent frequencies resulting from the exclusion process. The second row is the percent change from the original frequency. This list includes only those species in which a change was detected. Summed values listed here were standardized to a 0–100 range after analysis.

			Exclusion level (%)			
Species	Initial cover (%)	Plot type (cm^2)	0	10	20	30
Festuca idahoensis	7.7	250	26	24	22	20
				8	15	23*
		500	45	42	39	36
				7	13	20**
		1000	62	57	53	48
				8	15*	23**
		Sum	44	41	38	34
				7	14**	23**
Antennaria microphylla	2.3	250	24	22	20	18
				8	17	25*
		500	36	34	30	28
				6	17	22*
		1000	52	50	45	42
				4	13	19**
		Sum	37	36	32	29
				3	14**	22**
Lupinus caudatus	1.0	250	5	4	4	4
				20	20	20
		500	10	10	8	8
				0	20	20
		1000	18	14	12	10
				22	33*	44**
		Sum	11	10	8	7
				9	27**	36**
Agropyron spicatum	0.3	250	4	4	3	3
				0	25	25
		500	8	8	7	6
				0	12	25
		1000	15	12	10	8
				20	33	47**
		Sum	9	8	7	6
				11	22*	33**
Poa sandbergii	0.2	250	10	9	7	6
				10	30	40
		500	14	14	12	10
				0	14	29
		1000	20	19	17	14
				5	15	30*
		Sum	15	14	12	10
				7	20	30**
Apocynum androsaemifolium	1.7	250	8	8	8	6
				0	0	25
		500	14	12	11	10
				14	21	29
		1000	20	18	16	15
				10	20	25
		Sum	14	12	11	10
				14	21	29**
Frasera albicaulis	1.0	250	6	6	6	4
				0	0	33
		500	8	8	8	6
				0	0	25
		1000	18	16	16	14

Table 2 continued.

Species	Initial cover (%)	Plot type (cm^2)	Exclusion level (%)			
			0	10	20	30
				11	11	22
		Sum	10	10	10	8
				0	0	20*
Arenaria congesta	0.7	250	7	6	6	6
				14	14	14
		500	14	13	12	12
				7	14	14
		1000	20	18	17	16
				10	15	20
		Sum	14	13	12	11
				7	14	21*
Collinsia parviflora	0	250	6	4	4	2
				33	33	67
		500	12	10	10	8
				17	17	33
		1000	15	14	14	12
				7	7	20
		Sum	11	20	9	8
				9	18	27*
Stipa occidentalis	0	250	3	2	2	1
				33	33	67
		500	6	5	4	2
				17	33	67
		1000	8	8	6	6
				0	25	25
		Sum	6	5	4	3
				17	33	50**
Tragopogon dubius	0	250	2	2	1	1
				0	50	50
		500	2	2	2	1
				0	0	50
		1000	6	6	4	3
				0	33	50
		Sum	3	3	2	2
				0	33	33**

* Significant at $\alpha = 0.20$.
** Significant at $\alpha = 0.10$.

ble to detect a significant difference ($\alpha = 0.20$) in foliar cover when only 10% of the ground surface area was excluded (Table 1). However, at the 20% "exclusion level," all sites showed significant ($\alpha = 0.10$ for sites 1, 2, and 3; $\alpha = 0.20$ for site 4) reductions in foliar cover. When 30% of the ground surface area was excluded, all four sites showed significant ($\alpha = 0.10$) reductions in foliar cover when compared to their respective controls. These data provide additional information indicating that a change had occurred. Once it was known that a statistical change in cover had occurred, frequency data were analyzed.

Frequency

Except as noted, space considerations allow the frequency results from only the *Pinus ponderosa/Festuca idahoensis* habitat type to be reported. The results from the three other sites were similar.

Results from the chi-square analysis on frequency data are shown in Tables 2 and 3. Since the summation procedure used data from three plot sizes, a total summed "frequency" of 300% was possible. The chi-square analysis tested for significant changes in species occurrence over a potential range from 0

TABLE 3. Total number of herbaceous species which are significantly different ($\alpha = 0.20$) from the initial sample period at three exclusion levels for the 20 × 50 cm and summation plots.

Habitat type	Plot type (cm^2)	Exclusion level (%) 10	20	30
Pinus ponderosa/Festuca idahoensis	1000	0	2	5
	Sum	0	4	11
Artemisia tridentata subsp. *vaseyana/Festuca idahoensis* (unburned)	1000	0	3	5
	Sum	2	5	8
Artemisia tridentata subsp. *vaseyana/Festuca idahoensis* (burned)	1000	0	2	5
	Sum	0	4	10
Artemisia tridentata subsp. *vaseyana/Festuca idahoensis* (high elevation)	1000	0	2	5
	Sum	2	6	8

to 300 for the summed data, and 0 to 100 for the individual plot sizes. For ease of interpretation, the summed values were standardized, after analysis, to a maximum of 100%, consistent with the individual plot levels.

It should be recognized that data gathered with nested plots are not truly independent; a species recorded in a smaller plot is also in all larger plots. Theoretically, this may introduce a degree of bias. Under actual testing, however, this bias may not be significant. Hironaka (1985) demonstrated that separate, randomly placed frequency plot data were highly correlated ($R^2 = .998$) with nested plot frequency data. This suggests that the bias due to nested quadrats may be small and outweighed by the advantage of increased sensitivity.

Table 2 shows the results for the summation technique for the *Pinus ponderosa/Festuca idahoensis* habitat type. The table shows, by species, the relationship between initial frequency and the smallest subsequent change in frequency that is statistically different from the control. These changes were created by the three (10, 20, and 30%) exclusion levels. The summation technique detected a smaller change in frequency than any individual plot size at any given initial frequency. The summation technique was also able to detect changes in frequency in six additional species when 30% of the ground surface area was excluded. The additional species frequently had coverage values less than 2%, a value so small that changes were not detected with any single plot size.

The summation technique proved useful in increasing the resolution of range trend frequency data in several additional ways. The technique often detected a change with greater confidence at a lower alpha level (0.10 versus 0.20) than any single plot size (Table 2). For example, with *Festuca idahoensis* in Table 2, both summation and single-plot methods detected a 15% change in frequency. Furthermore, the summation technique detected this change at a probability level of 0.10, whereas the single-plot difference was significant at the $\alpha = 0.20$ level only. The summation technique detected change at a lower initial frequency than any single plot size (Table 2). Using the summation process would be advantageous when attempting to detect change in species having lower frequency values. Compared to any individual plot size, the summation procedure detected significant changes in an average of four additional species per site (Table 3). Detecting change in a greater number of species at smaller amounts of change adds credibility and confidence to any judgment about range trend.

The use of summed frequencies can be an advantage also when the change is relatively large. For example, if a particular species of interest was becoming more numerous over time, the smaller plots included in the nested plot configuration would help prevent the resulting "frequency" value from truncating at 100 in subsequent measures. Even though one or more of the larger plots in the configuration might reach 100% frequency as the species became more numerous, it would be unlikely for one of the smaller plots to do so at the same time. When the frequencies of all the plot sizes are added together, the presence of the smaller plot's frequency will prevent the summed total from reaching 300% "frequency" (assuming three plot sizes are used).

If, instead, a single plot had been used to monitor the same species, it would be initially advantageous to use a plot size giving an initial frequency of 20 to 80%. However, if the species increased in density and the frequency at any succeeding sample reached 100%, subsequent increases in that species could not be detected. Since the influence of the smaller plot sizes on the summed total is inherent, the summation technique would eliminate the need to change plot size over time as a species experienced major changes in density. Therefore, using the sums of nested plots provides more sensitivity to vegetational change over a wider range of species abundance than any single plot.

Smith et al. (1986) noted that initial frequency and magnitude of ensuing changes are the main factors controlling the sensitivity of frequency plots to vegetational change. This also held true when the change being sampled used the sums of nested plots. As initial frequency and/or percentage change increased, so did the ability of the nested frequency plots to detect that change. Detection of small percentage changes required a large initial frequency. It was rare to detect a 10% change if the initial frequency was less than 60%, but a 30% change was often detected when the initial frequency was less than 15%.

CONCLUSION

Frequency data are highly correlated with plot size. Although frequency data gathered with a single plot size are easiest to analyze, no one plot size can adequately sample a wide variety of plant species at the same time. This study examined the possibility of summing data from three different plot sizes, arranged in a nested configuration, in an effort to further improve the sensitivity and efficiency of frequency as a method for detection of trend.

For the four sites studied, summation of frequencies provided greatest sensitivity to vegetational change. Such changes in summation values were shown to be significant at lower alpha levels than for any single plot within the nested configuration. These results were consistent over a wide range of frequencies. In addition, summation was superior for detecting changes in species having low initial frequencies and foliar coverages. Finally, the summation technique detected significant changes in more species than did any single plot size.

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NOTES ON MYCOPHAGY IN FOUR SPECIES OF MICE IN THE GENUS *PEROMYSCUS*

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ABSTRACT.—Fungal spores in the stomach contents and/or feces of 696 *Peromyscus* spp. showed that about half had eaten fungi: of 486 deer mice (*P. maniculatus*), 48%; of 160 white-footed mice (*P. leucopus*), 59%; of 40 canyon mice (*P. crinitus*), 12%; and of 10 piñon mice (*P. truei*), 90%.

Although much has been written about the genus *Peromyscus*, especially *P. maniculatus* and *P. leucopus*, relatively little has been written about their food habits. King's (1968) book on the genus *Peromyscus* does not consider food habits. Deer mice (*P. maniculatus*) have long been considered a problem in reforestation in the Pacific Northwest (Gashwiler 1965, 1979, Hooven 1958, Sullivan 1979a, b). Most studies on food habits lack information on fungi (e.g., Cook et al. 1982, Douglas 1969, Flake 1973, Halford 1981, Lackey et al. 1985, Osborne and Sheppe 1971). Some studies include fungi as one of many kinds of foods eaten (e.g., Martell and Macaulay 1981, Merritt and Merritt 1980, Schloyer 1976, Whitaker 1966, Williams 1959). A few studies deal specifically with fungi in the diet of *Peromyscus* (e.g., Harling and McClaren 1970, Hunt and Maser 1985, Maser et al. 1978).

In this study we examine hypogeous, mycorrhizal fungi in the diet of four members of the genus *Peromyscus*. Our intent was a survey of fungal use by particular members of the genus *Peromyscus* to ascertain their potential functional dynamics within the habitat. Although it has taken more than 10 years to gather enough material, our study has some deficiencies because some animals were collected in fungal fruiting seasons whereas others were not. Also, little study has been done with mycophagy in grassland and shrub-steppe habitats; in fact, little is known about hypogeous fungi in such environments (Trappe 1981). The data we present are new, and they should help us understand the functional role of wide-ranging, highly adaptable small mammals in their respective habitats.

METHODS AND MATERIALS

The 696 mice used in our study were snap-trapped over widely scattered areas in North America. Most specimens were quick-frozen in the field for later analysis. Of the mice, 324 (collected by us) were analyzed for fungi by stomach content, and 372 (collected by others for us) were analyzed by fecal content. Both stomach contents and feces were preserved in vials of 10% formalin.

Stomach contents and feces were microscopically examined at 100, 400, and 1,000X magnification. A small amount of equally mixed material was randomly sampled from each vial with narrow, parallel-sided forceps, placed on a microscope slide, mixed with a drop of Melzer's reagent (I, KI, and chloral hydrate), and enclosed under a 22 x 40 mm cover slip. The slide was systematically examined for fungal spores. Fungal taxa were identified with the aid of a spore key (Trappe et al., in prep.). We use percent frequency because percent volume cannot be used for fecal analysis.

RESULTS AND DISCUSSION

Twenty-seven fungal taxa were identified from the 696 mice examined: *P. maniculatus* contained 22 taxa (Table 1), *P. leucopus* 18 taxa (Table 2), *P. truei* 11 taxa (Table 2), *P. crinitus* 1 taxon (Table 2).

The Mice

Peromyscus maniculatus (deer mouse). There were 209 *P. maniculatus* examined

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TABLE 1. Percent frequency of fungal taxa from 486 *Peromyscus maniculatus*.

Fungal genera	Western Oregon (n=209)	Western Washington and southwest British Columbia (n=92)	Northeast Oregon (n=27)	Southeast Oregon (n=128)	Iowa (n=19)	Ontario, Canada (n=11)
ASCOMYCETES						
Hypogeous						
Balsamia	2					
Cenococcum	1	2				
Choiromyces	1					
Elaphomyces	2					
Genabea	1					
Genea	5					
Geopora	1					
Hydnotrya	2					
Picoa	3					
Tuber	2		33		5	
BASIDIOMYCETES						
Hypogeous						
Gautieria	4					
Octavianina	2					
Hymenogaster	7	1			5	
Hysterangium	2					
Leucogaster	3					
Leucophleps	1					
Martellia group	1					
Melanogaster	2					
Rhizopogon	25	1	19		5	
ZYGOMYCETES						
Hypogeous						
Endogone	3	7				
Glomus	21	35	8	17	32	100
Sclerocystis	1	5				
OTHER FUNGI						
Unidentified	6	7	4	14	11	
LICHEN						
Unidentified	1					

from western Oregon forests (Table 1), and 22 fungal taxa were found. The mice were from Douglas-fir (*Pseudotsuga menziesii*) forests where they are known to be mycophagists (Hunt and Maser 1985). Although a wide variety of fungi was eaten, *Rhizopogon* and *Glomus* had a disproportionately high percent frequency of consumption (25 and 21, respectively).

Peromyscus maniculatus from western Washington and southwestern British Columbia ate seven fungal taxa (Table 1). Most of these mice were in riparian habitats. Three fungal taxa in the family Endogonaceae had 47% frequency, whereas others had 7% frequency and a small number (4) of other fungal taxa. The three genera *Endogone*, *Glomus*, and *Sclerocystis* (family Endogonaceae) also represented the three highest percent frequencies (7, 35, and 5, respectively).

Peromyscus maniculatus in northeastern Oregon had eaten fungi of three taxa (Table 1). *Tuber* sp., with 33% frequency, was gleaned from the bluebunch wheatgrass (*Agropyron spicatum*)–Idaho fescue (*Festuca idahoensis*) habitat; the next highest percent frequency (19) was *Rhizopogon* from mice caught in the lodgepole pine (*Pinus contorta*) habitat.

Little fungus was found in the stomachs of 128 *Peromyscus maniculatus* from the arid sagebrush (*Artemisia* spp.) steppe of southeastern Oregon (Table 1). The only identifiable taxon was *Glomus* at 17% frequency.

TABLE 2. Percent frequency of fungal taxa from 210 *Peromyscus* spp.

Fungal genera	*P. leucopus* (n = 160)	*P. truei* (n = 10)	*P. crinitus* (n = 40)
ASCOMYCETES			
Hypogeous			
Balsamia	1	10	
Barssia	1		
Choiromyces	4		
Elaphomyces	3	10	
Genea	3	20	
Geopora	6	10	
Hydnobolites	1		
Picoa	3		
Tuber	5	10	
BASIDIOMYCETES			
Hypogeous			
Gautieria	1	10	
Octavianina	1	20	
Hymenogaster	13	10	
Leucogaster	1	20	
Melanogaster	1		
Rhizopogon	20	70	
ZYGOMYCETES			
Hypogeous			
Endogone	3		
Glomus	25	10	3
Sclerocystis	1		
OTHER FUNGI			
Unidentified	14	20	11

Peromyscus maniculatus from Iowa and Manitouwadge, Ontario, Canada, also concentrated on fungi of the genus *Glomus*, with a 32 and 100% frequency, respectively (Table 1). The stomachs of the *P. maniculatus* from Manitouwadge contained *Glomus* in the following amounts: 10 mice, 100%, and 1 mouse, 95% by volume. These mice were trapped in a black spruce (*Picea mariana*) forest.

Peromyscus leucopus (white-footed mouse).—All 160 *P. leucopus* examined from Iowa were trapped in wooded habitats (Table 2). The mice had eaten fungi of eight taxa, percent frequency 1; and three taxa, percent frequency greater than 10. The family Endogonaceae (*Endogone*, *Glomus*, and *Sclerocystis*) had 28% frequency, and *Rhizopogon*, an obligatory symbiont with Pinaceae, had 20% frequency.

Peromyscus truei (piñon mouse).— Ten *P. truei* from southwestern Oregon had consumed fungi of 11 taxa, ranging from 10 to 70% frequency (Table 2). These mice were trapped in mixed conifer-hardwood forest, a habitat different from the rangeland habitat that *P. truei* is associated with throughout most of its geographical distribution.

Peromyscus crinitus (canyon mouse).— Forty *P. crinitus* were collected in the arid sagebrush canyonlands of southeastern Oregon. Because little is known about the fungi of the sagebrush steppe of southeastern Oregon, only one genus, *Glomus*, could be identified with certainty (Table 2).

The Fungi

Mycorrhizal fungi absorb nutrients and water from soil and translocate them to a host plant. The host provides sugars from photosynthesis to the mycorrhizal fungi. Fungal hyphae extend into the soil and serve as extensions of the host root systems and are both physiologically and geometrically more effective for nutrient absorption than the roots themselves (Maser et al. 1978, Trappe 1981, Trappe and Fogel 1977, Trappe and Maser 1977). Both ectomycorrhizal and endomycorrhizal fungi serve similar purposes, but they usually occur on different host plants.

When ectomycorrhizal fungi are predominant in the fungal diet of small mammals, they are also predominant in the habitat, such as coniferous forests. There they are mostly Ascomycetes and Basidiomycetes associated with Pinaceae, Fagaceae, Salicaceae, Betulaceae, and a few other plant families (Fogel and Trappe 1978, Maser et al. 1978, Trappe and Maser 1977).

The Endogonaceae (Zygomycetes) include saprophytic, ectomycorrhizal, and vesicular-arbuscular (VA) endomycorrhizal species. Vesicular-arbuscular mycorrhizae are formed by Endogonaceae with most higher plants that are not ectomycorrhizal, including the Cupressaceae, Taxodiaceae, Aceraceae, and most herbaceous plants. Most plants on streambanks, meadows, prairies, in early stages of forest succession, forest understories, or forests containing VA-mycorrhizal tree species have VA-mycorrhizal Endogonaceae associated with their roots (Maser et al. 1978, Miller 1979, Reece and Bonham 1978, Trappe 1981, Williams and Aldon 1976). Sampling in such habitats showed that the fungi of highest frequency were VA-mycorrhizal taxa.

Interactions

Tables 1 and 2 show that Endogonaceae

(*Endogone*, *Glomus*, and *Sclerocystis*) is a dominant fungal component in the diet of *Peromyscus maniculatus* and *P. leucopus* at certain times. Similar conclusions can be derived from other studies (e.g., Gerdemann and Trappe 1974, Hamilton 1941, Harling and McClaren 1970, Martell and Macaulay 1981, Schloyer 1976, Whitaker 1966, Williams and Finney 1964). Both mice, however, are basically opportunistic (Lackey et al. 1985, Merritt and Merritt 1980).

Whitaker (1966, 1967) found that *Peromyscus leucopus* in Indiana lives essentially in wooded habitat, whereas *P. maniculatus* occupies primarily nonwooded habitat. This may account for the 15 taxa of hypogeous, ectomycorrhizal Ascomycetes and Basidiomycetes in the diet of *P. leucopus* from Iowa (Table 2) compared with the 3 taxa of these fungi in the diet of *P. maniculatus* from Iowa. Hypogeous Ascomycetes and Basidiomycetes tend to produce relatively large, odoriferous sporocarps, whereas Zygomycetes (Endogonaceae) produce small sporocarps with slight odor or none. Howard and Cole (1967) and Howard et al. (1968) demonstrated that *P. maniculatus* not only has an excellent sense of smell but also relies on this sense to detect food. Acute olfaction, coupled with nonwooded or lightly wooded habitat over much of its range, may help explain the apparent selectivity by *P. maniculatus* for fungi in the Endogonaceae.

The four species of *Peromyscus* appear to be opportunists in diet (Douglas 1969, Drickamer 1976, Whitaker 1966, 1967, Wilson 1968). In nonforested areas their concentration on VA-mycorrhizal fungi as food can help plants that require such mycosymbionts because the mice disperse viable spores through defecation (Rothwell and Holt 1978, Trappe and Maser 1976). The same would be true in coniferous forests where dispersal of VA-mycorrhizal spores by mice would enhance establishment of early successional and understory vegetation. Our laboratory data also show that spores of ectomycorrhizal fungi (in coniferous forests) are viable after passage through the intestinal tracts of *P. maniculatus*. Other rodents appear to be more important, however, than *P. maniculatus* for dispersal of ectomycorrhizal spores in coniferous forests (Kotter and Farentinos 1984, Maser et al. 1978, 1985, Trappe and Maser 1977, Ure and Maser 1982).

Perhaps the main importance of mycophagy by members of the genus *Peromyscus* is that, to some extent, they are connoisseurs of endomycorrhizal fungi in the Endogonaceae. This is potentially important, particularly in nonforested habitats, because these mice may play a role in plant succession by dispersing viable spores on vegetating mining spoils (Aldon 1975, Rothwell and Holt 1978), by helping native vegetation become established in severely disturbed areas that are inhabited primarily by a few Old World, nonmycorrhizal species (Miller 1979), and by helping to maintain already-established healthy native plants (Green et al. 1983, Molina et al. 1978, Reece and Bonham 1978, Williams and Aldon 1976).

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BEE VISITORS OF SWEETVETCH, *HEDYSARUM BOREALE BOREALE* (LEGUMINOSAE), AND THEIR POLLEN-COLLECTING ACTIVITIES[1]

Vincent J. Tepedino[2] and Mark Stackhouse[3]

Abstract.—The native bee fauna visiting and pollinating a population of sweetvetch in Grand Teton National Park was surveyed. The papilionaceous flowers were exploited by 37 bee species, most of which had long mouthparts. Most species collected pollen as well as nectar. Bees foraged most heavily in early afternoon when pollen was most abundant. However, there was no indication that bee species were competing for limited pollen resources: there was no difference among three time periods in percent sweetvetch pollen carried in the scopal pollen loads of bees nor was there any evidence that some species were displacing the foraging times of others. The advantages of developing a native species as a commercial pollinator of sweetvetch are discussed and several potential candidates are mentioned.

Legumes are important components of rangeland ecosystems because of their ability to enrich the soil by fixing nitrogen and because of the nutritional content and palatability of some to livestock and wildlife. These characteristics have led to suggestions that productivity of rangelands can be increased by using mixtures of grasses and legumes rather than grasses alone (Cook 1983, Rumbaugh and Townsend 1985).

Among the many species of legume under study for potential inclusion in the managed rangeland community is sweetvetch, *Hedysarum boreale* Nutt., a perennial forb of holarctic distribution. Sweetvetch fixes nitrogen and is both nutritious and palatable to grazing animals (Rumbaugh and Townsend 1985). Two subspecies grow in North America: ssp. *boreale* in the western United States and southern British Columbia and Alberta; and ssp. *mackenzii* in northern Canada, the Yukon Territory, and Alaska (Northstrom and Welsh 1970). Subspecies *boreale* is likely to be most valuable as a rangeland plant because of its geographic distribution and habitat requirements.

Although sweetvetch is an excellent seed producer (Rumbaugh and Townsend 1985), seed for use in rangeland seedings and in revegetating disturbed sites is both costly and scarce. At present, seed is primarily collected from wild plants in natural habitats; commercial production has hardly begun. Indeed, aside from a study of ssp. *mackenzii* in the Yukon Territory (Kowalczyk 1973), there is little known of the reproductive biology and pollination ecology of sweetvetch. Kowalczyk (1973) reported that in ssp. *mackenzii* the pinkish to purple papilionaceous flowers were partially self-fertile but required visitation by insects, particularly bumblebees (*Bombus*), to set seed. The pollination ecology of ssp. *boreale* may differ because the flowers are smaller than those of ssp. *mackenzii* (Northstrom and Welsh 1970) and may be less attractive to long-tongued bumblebees.

This study describes the bee fauna visiting a natural population of *Hedysarum boreale boreale* in Grand Teton National Park, Wyoming. In particular, we report on the relative abundances of bee visitors at different times of day and their pollen-collection activities.

METHODS

We selected an undisturbed population of several hundred *Hedysarum boreale boreale* growing among *Artemisia tridentata* and other subshrubs on the rocky, south- and west-facing slopes of Spread Creek Hill, Teton Co., Wyoming, at about 2,200 m altitude. Systematic collections of bees were made on five days from late June to mid-July during the peak blooming period. To assure a representative temporal sample of flower visitors, two collectors were active during each of

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TABLE 1. Total number of bees captured by species and number of females captured by time period (N). P - number of females carrying pollen; % pollen is the average percent sweetvetch pollen carried in the scopa.

	Total no. bees captured		No. females captured Time period			
			1	2	3	No time recorded
	♂♂	♀♀	N (P) % Pollen	N (P) % Pollen	N (P) % Pollen	N (P) % Pollen
Andrenidae						
Andrena spp.	1	2				2 (0)
Anthophoridae						
Nomada spp.	1	0				
Tetralonia frater (Cresson)	3	101	27 (18) 79.1	42 (33) 80.7	18 (16) 79.8	14 (14) 87.1
Apidae						
Apis mellifera Linnaeus	0	7				7 (0)
Bombus appositus Cresson	0	5				5 (0)
Bombus bifarius Cresson	0	11				11 (5)
Bombus fervidus (Fabricius)	0	3				3 (1)
Bombus flavifrons Cresson	0	19				19 (5)
Bombus griseocollis (Degeer)	0	7				7 (0)
Bombus nevadensis Cresson	0	13				13 (0)
Bombus occidentalis Greene	0	2				2 (0)
Bombus rufocinctus Cresson	0	10				10 (4)
Bombus sylvicola Kirby	0	1				1 (1)
Psithyrus insularis (Smith)	0	2				2 (0)
Halictidae						
Evylaeus spp.	0	2				2 (0)
Halictus spp.	1	0				
Megachilidae						
Callanthidium formosum (Cresson)	1	0				
Hoplitis albifrons (Kirby)	1	1				1 (0)
Hoplitis producta (Cresson)	0	1				1 (0)
Megachile frigida Smith	3	7	0	6 (6) 76.4	1 (0)	
Megachile gemula Cresson	5	15	2 (2) 76.9	8 (7) 73.7	2 (2) 90.6	3 (3) 86.7
Megachile inermis Provancher	1	0				
Megachile melanophaea Smith	5	34	8 (6) 87.1	15 (11) 86.3	10 (5) 88.3	1 (1) 89.6
Osmia albolateralis Cockerell	3	17	2 (1) 96.0	11 (11) 87.6	4 (4) 99.1	
Osmia atrocyanea Cockerell	0	4	2 (2) 75.2	1 (1) 96.3	1 (1) 67.0	
Osmia bruneri Cockerell	0	5	2 (2) 29.3	3 (3) 89.5		
Osmia bucephala Cresson	0	21	3 (3) 65.9	12 (12) 73.8	5 (5) 81.6	1 (1) 90.3
Osmia cockerelli Sandhouse	1	0				
Osmia grindeliae Cockerell	2	9	2 (2) 98.2	5 (5) 96.4	1 (1) 99.7	1 (1) 99.0
Osmia inermis (Zetterstedt)	0	3		1 (1) 98.3	1 (1) 98.0	1 (1) 98.3
Osmia longula Cresson	2	5		3 (3) 96.1	1 (1) 90.0	1 (1) 94.0
Osmia nifoata Cockerell	1	1		1 (1) 42.6		
Osmia paradisica Sandhouse	0	10	5 (3) 72.5	3 (3) 69.5		2 (1) 79.0
Osmia pentstemonis Cockerell	0	4	1 (1) 93.6	3 (1) 43.3		
Osmia pusilla Cresson	0	5	1 (1) 88.0	3 (1) 79.6		1 (1) 86.6
Osmia tersula Cockerell	0	2	1 (1) 60.3	1 (0)		
Osmia tristella Cockerell	0	1	1 (1) 1.0			
TOTALS	31	330	57 (43)	118 (99)	44 (36)	110 (40)
$\overline{X}$			78.4%	84.0%	86.2%	

three 80-minute time periods each day, once in the morning from 940 to 1100 hr, once in the afternoon, usually from 1440 to 1600 hr, and once in early evening between 1900 and 2200 hr.

Insects were netted while they foraged on the flowers. After insects were pinned and labeled, pollen slides were made from all solitary bees carrying pollen in their scopae. Pollen from each of the hind legs or venter (in the case of megachilids) was scraped onto a clean slide with an insect pin and stained as described by Beattie (1971). Except where noted, 300 grains from each slide were identified under 450X magnification by comparison with a pollen-reference collection. (For bumblebees, we merely noted whether they were carrying pollen.)

RESULTS

Sweetvetch proved to be highly attractive to bees, especially to those with long mouthparts. During 40 man-hours, we collected 37 species of bees, most in the family Megachilidae (21), in the genera *Osmia* (14) and *Megachile* (4) (Table 1). Bumblebees (*Bombus* and *Psithyrus;* Apidae) were also common (10 species). Most abundant was another species with long mouthparts, *Tetralonia frater* (Cresson) (Anthophoridae). Only 3 species (6 individuals) with short mouthparts, in the families Andrenidae and Halictidae, were collected.

The most abundant species captured were collectors of sweetvetch pollen, although a few (e.g., *Bombus griseocollis* (Degeer), *B. nevadensis* Cresson) seemed primarily collectors of nectar. Of 178 pollen samples examined (all from species in the families Anthophoridae and Megachilidae), 147 (82.6%) contained at least 75% sweetvetch pollen. Thus, individuals that foraged on sweetvetch were quite flower constant, at least within individual foraging trips.

The time of day that bees forage for floral rewards is influenced by such factors as ambient temperature, time of nectar and pollen production, and schedule of availability of flower rewards from competing species (Linsley 1978). For any given flower species, bee foraging is not usually spread evenly throughout the day but is restricted to the most rewarding times. In sweetvetch, as in many other legumes (Frankel and Galun 1977), the anthers of the diadelphous stamens dehisce simultaneously in the bud, and pollen is available at anthesis, usually in mid to late morning, after our first collection period. We used this schedule to make two predictions about bee foraging: (1) flower visitation is highest during the second collection period; and (2) because pollen in flowers should be gradually depleted over the course of a day, the percentage of sweetvetch pollen in the pollen loads of bees should be highest during the second collection period and lowest during the first collection period.

The data supported only the first of these hypotheses. Significantly more bees visited the flowers for nectar and/or pollen during the second collection period than during the first or third collection periods ($X^2 = 40.2$, d.f. $= 2$, $P < 0.001$; Table 1). The distribution over time of bees collecting pollen followed the same pattern ($X^2 = 42.8$, d.f. $= 2$, $P < 0.001$). There was no difference in the distributions between bees that were collecting pollen and those that were not ($X^2 = 1.8$, d.f. $= 2$, $P > 0.25$). These results held for all abundant bee species; there was no indication that any species specialized in foraging at a particular time or that time was a resource which bees were partitioning.

Our second prediction, that the percentage of sweetvetch pollen in the pollen loads would be highest during the second collection period, was not supported by the data; When all pollen-collecting bees were grouped, irrespective of species, there were no differences among time periods in the percentage of sweetvetch pollen in bee pollen loads (ANOV on arcsin transformed data: $F = 1.89$, d.f. $= 2{,}175$, $P = 0.15$). This result also held when the more abundant species were examined individually: for *Tetralonia frater*, the mean percentage of sweetvetch pollen ranged only from 78.7% to 80.1% across the three time periods. Results for other species such as *Megachile gemula* Cresson, *M. melanophaea* Smith, and *Osmia bucephala* Cresson were similar.

DISCUSSION

In Grand Teton National Park, sweetvetch flowers are very attractive to a variety of bee species with long mouthparts (Table 1). This is not surprising because the long, narrow, closed corolla tube of papilionaceous legume flowers makes their rewards, particularly nectar, unavailable to species with short mouthparts.

Our collections on ssp. *boreale* in the Tetons yielded a far more diverse bee fauna than that found by Kowalczyk (1973) on ssp. *mackenzii* in the Yukon Territory. In the Yukon, ssp. *mackenzii* was visited and pollinated almost exclusively by bumblebees. Indeed, the *Osmia*, *Megachile*, and *Anthidium* that Kowalczyk (1973) did find were so rare that he did not even bother to have them identified to species. While bumblebees were also abundant on sweetvetch flowers in the Tetons, other species with long mouthparts were more numerous. The most straightforward explanation for this difference is simply that bumblebees comprise an increasing proportion of the bee fauna with increasing latitude (Morse 1982). This transition is a result of an increase in bumblebee numbers with latitude but rather to a gradual decline in the diversity and abundance of solitary species, presumably because of their inability to adapt to the harsh climate.

It is not farfetched to speculate that the decline, with increasing latitude, of solitary bee pollinators of sweetvetch has influenced the length of the corolla in ssp. *mackenzii* and may have played a role in its separation from ssp. *boreale*. Indeed, pollinators have been implicated as agents of speciation in many plant taxa (Levin 1971). We suggest that the longer corolla in ssp. *mackenzii* gradually evolved as an adaptation to the larger, and more abundant and reliable, bumblebee pollinators whose mouthparts are generally longer than those of solitary species. As the corolla lengthened over time, the flowers would gradually become less exploitable by solitary species until, eventually, only bumblebees could forage from them with consistent profit. There would be no such selective pressure on ssp. *boreale* because of the size, diversity, and reliability of nonbumblebee populations.

Should sweetvetch prove to be a desirable species for rangeland seedlings or revegetating disturbed areas, commercial seed-growing operations will be needed. Depending on the area and situation under which commercial operations are conducted, it may be necessary to provide a pollinating insect to obtain maximum seed production. If the area under cultivation is small and is adjacent to natural habitat, then it is probable that sweetvetch is sufficiently attractive to native bees to require no special provision for pollination. For example, a three-acre planting surrounded by rangeland in western Wyoming attracted numerous megachilid and apid species and produced copious seed. If plantings are larger or are located in cultivated areas where bees are scarce, it may be necessary, or desirable, to develop a solitary bee species that can be managed as a commercial pollinator. Pollination by solitary species would be especially appropriate for sweetvetch because plantings are likely to be relatively small and bloom lasts only about a month. Thus, a pollinator that has but one generation a year and flies for a short period of time (a few weeks) would be ideal. Small populations should also be readily obtainable, and the bee should be attracted to the plant. Obviously, several species listed in Table 1 possess these characteristics. Of these, some are particularly amenable to manipulation because they nest in existing holes in wood (Parker and Torchio 1980). Examples are *Megachile gemula* and *Osmia albolateralis* Cockerell, *O. bruneri* Cockerell and *O. bucephala*. Such species require minimal care and attention because they spend 10 to 11 months of each year as immatures in their nests. Any attempt to develop a solitary bee as a commercial pollinator for sweetvetch would do well to begin with one of these species.

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OBSERVATIONS ON NATURAL ENEMIES OF WESTERN SPRUCE BUDWORM (*CHORISTONEURA OCCIDENTALIS* FREEMAN) (LEPIDOPTERA, TORTRICIDAE) IN THE ROCKY MOUNTAIN AREA

Howard E. Evans[1]

ABSTRACT.—Three species of predators and parasites were found associated with western spruce budworm (*Choristoneura occidentalis* Freeman) (Lepidoptera, Tortricidae) in Larimer Co., Colorado. These were: *Ancistrocerus antilope* (Panzer) (Hymenoptera, Vespidae), *Goniozus gracilicornis* (Kieffer) (Hymenoptera, Bethylidae), and *Ceromasia auricaudata* Townsend (Diptera, Tachinidae). The first two species stored caterpillars in wooden trap nests, while the third was reared from final instar budworms.

Over the past several years I have had an opportunity to observe several predators and parasites of the western spruce budworm (*Choristoneura occidentalis* Freeman) near my home, 23 km west of Livermore, Larimer Co., Colorado. This is an area of open ponderosa pine–Douglas-fir forest at 2,300 m elevation. Spruce budworms occur here regularly on Douglas-fir, in some years causing extensive damage and sometimes tree mortality. Infestations were, however, moderate to low during the period of study (1985–1986). Budworms attain final instar during June and pupate in early July.

METHODS

Some records were obtained by collecting and rearing last instar larvae, but more were obtained from trap nests. Trap nests consisted of pieces of pine 15 cm long and 2 cm square, with a groove (6 or 9 mm in diameter) on one side to which a strip of Plexiglas was taped. A wooden strip was then placed over the Plexiglas; the strip could easily be removed for examination of trap nest contents. Traps were placed 0.3 to 2.5 m above the ground in wood piles or in living or dead trees or attached to my house. They were accepted by several species of bees and wasps, the most abundant of which were two species of *Ancistrocerus*, *adiabatus* (Saussure) and *antilope* (Panzer) (Vespidae, Eumeninae). Both are well-studied species that make a series of cells separated by mud partitions and provisioned with larvae of Microlepidoptera (references in Krombein 1979). Only *A. antilope* used spruce budworms as prey.

RESULTS

Ancistrocerus antilope **(Panzer)** (Vespidae). Eleven trap nests with a total of 49 cells were provisioned by females of this species in 1985 (none in 1986). Nests with bores of 6 to 9 mm were accepted, cell lengths varying from 8 to 18 mm (mean 11.8, N = 30) in bores of 8 to 9 mm and from 13 to 22 mm (mean 18.0, N = 19) in bores of 6-mm diameter. Each nest had an outer, empty vestibular cell measuring from 8 to 31 mm in length, as well as an outer closure. No accurate count of prey was made in all cells, but of 8 counted the mean was 5.5 per cell. Thus, the total prey in the 11 nests approximated 270 Microlepidoptera. Of these, 20 (7.4%) were *Choristoneura occidentalis*, the remainder several other species of Microlepidoptera. However, 7 of the 11 nests were provisioned after most of the budworms had pupated. Of 4 nests provisioned prior to 3 July, 8 of the 15 cells contained spruce budworms; 24% of the prey consisted of that species. One nest of 4 cells contained 16 budworms (4 per cell), while another of 3 cells contained 3 budworms and 15 other larvae. After 3 July, no spruce budworms were found in any of the nests.

Two nests had cells parasitized by cuckoo wasps, *Chrysis coerulans* Fabricius, and two had cells parasitized by flies of the genus *Amo-*

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bia (Sarcophagidae). Both have been reared from *Ancistrocerus antilope* previously (Krombein 1967). Three ichneumon wasps, *Pimpla spatulata* Townes, also emerged from one nest. This species was reared by Krombein (1967) from members of two other genera of Vespidae (Eumeninae) in New York.

In eastern North America, spruce budworms (*Choristoneura fumiferana* [Clemens]) have been found to serve as prey of eumenine wasps on several occasions. Fye (1962, 1965) recorded *Ancistrocerus adiabatus* (Saussure), *A. catskill* (Saussure), and *Euodynerus leucomelas* (Saussure) preying on budworms in Ontario. He felt that it might be possible to take advantage of the wasp's searching abilities to sample populations of this and other species of Microlepidoptera. Jennings and Houseweart (1984) found *A. catskill* and *E. leucomelas* provisioning trap nests with spruce budworms in Piscataquis Co., Maine. *Ancistrocerus antilope* also accepted their traps but provisioned only with *Nephoterix* sp. (Pyralidae). Western spruce budworms have not previously been reported as prey of *A. antilope*.

Goniozus gracilicornis **(Kieffer)** (Bethylidae). On 5 July 1986 I collected a trap nest (3-mm-diameter bore) that contained three cells of a species of *Trypoxylon* (Sphecidae). The cells were at the inner end of the bore, each containing paralyzed spiders and a wasp egg and closed off with a mud partition. Outside of the last partition but 60 mm from the bore opening (which had not been closed) was a paralyzed last instar larva of the western spruce budworm. The larva was 19 mm long and of a thickness such that it barely fit within the trap nest. It bore 20 elongate eggs, each about 0.8 mm long. They were attached longitudinally over much of the dorsal length of the thorax and abdomen. The eggs had not hatched on the following day. However, five days later the larvae had already completed their development, and the remains of the caterpillar were covered with white, silken cocoons. (I was away during these five days and did not observe the progress of the larvae.) Sixteen days later nine female *Goniozus gracilicornis* appeared in the rearing container. I suspect that several more of these minute, flattened wasps had escaped from the container.

It remains a puzzle as to how the budworm larva had been placed in a trap nest with a bore this small. The trap nest had been attached to a ponderosa pine branch, about a meter above the ground. Pines usually are not hosts of spruce budworms; presumably the larva came from a nearby Douglas-fir. The bethylid wasps measure about 3 mm long, and it is difficult to conceive of a female wasp dragging a prey this large any distance. However, there are records of Bethylidae of several genera dragging their prey into places of concealment, even though the prey was commonly much larger than the wasp (Yamada 1955, Rubink and Evans 1979). Gordh (1976) remarked that species of *Goniozus* have not been observed moving their prey, but he did note a female *G. gallicola* Fouts attempting to drag paralyzed prey to the side of a container. Also, the type specimen of *G. raptor* Evans was taken "carrying larva of pink bollworm by the head" (Evans 1978). The ability of bethylids to drag their paralyzed prey into a protected place may account for the fact that several species have been reared from stems and galls.

Goniozus gracilicornis has been reared from species of Gelechiidae and Tortricidae (Evans 1978), but from species attacking crop plants rather than trees. Another species of *Goniozus*, *floridanus* (Ashmead), has been reared from *Choristoneura rosaceana* Harris, which attacks broad-leafed trees. Most species of *Goniozus* not only parasitize a variety of Microlepidoptera but also occur in diverse habitats. *Goniozus gracilicornis* is not listed as a parasite of western spruce budworms in Oregon by Carolin and Coulter (1959).

Ceromasia auricaudata **Townsend** (Tachinidae). In 1985 and again in 1986 I collected 20 final instar larvae of western spruce budworm and reared adults from them. In each year two tachina flies also emerged; all four were *Ceromasia auricaudata*. This species was one of the more prevalent of 10 tachinid species reared from *Choristoneura occidentalis* in Oregon (Carolin and Coulter 1959). Despite the small sample size, it seems safe to categorize this species as one of the more important parasites of the western spruce budworm in the east central Rocky Mountain area.

DISCUSSION

Although these studies were made casually in the course of other research, they add a few details to the extensive literature on the natural enemies of the western spruce budworm. Jennings and Crawford (1985) suggest several ways in which the effect of natural enemies can be enhanced, such as providing an abundance of flowering plants that serve as nectar sources and providing nest boxes for birds. In the Rocky Mountain area, mountain chickadees, which are major predators on larvae, readily accept nest boxes. Trap nests for wasps can also be made cheaply and, if placed in the field well before budworms pupate, can provide a means of assessing budworm abundance. Trap nests may also provide homeowners with an additional means of protecting their trees.

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PLANT COMMUNITY ZONATION IN RESPONSE TO SOIL GRADIENTS IN A SALINE MEADOW NEAR UTAH LAKE, UTAH COUNTY, UTAH

Jack D. Brotherson[1]

Abstract.—Patterns of zonation along a saline meadow slope were studied. Different species associations were distributed in five zones along the slope which paralleled Utah Lake. The five zones, distinguished on the basis of dominant species and/or life form, were: saltgrass–annual weed, saltgrass-alkaligrass, saltgrass-forb, saltgrass, and spikerush. Soil, vegetation, and plant species data were taken. Patterns of change with respect to these factors were observed along the downslope gradient. Soil pH and soluble salts decreased downslope, while organic matter and moisture increased. Individual ions showed varying patterns. Vegetation and species patterns also varied with slope position. Annuals dominated the ridge tops, while sedge and rush cover were restricted to the slope base. Perennial forb distribution was shown to be correlated with elevated levels of micronutrients in the soil.

The ecological relationships of halophytic species and their communities within coastal environments are well investigated (Adams 1963, Vogl 1966, van der Maarel and Leertouwer 1967, Cotnoir 1974, Daiber 1974, Duncan 1974, Godfrey et al. 1974, Hinde 1954, Kraeuter and Wolf 1974, MacDonald and Barbour 1974, Walsh 1974), but less has been done on inland halophytes and their communities (Ungar 1969, Chapman 1974, Hansen and Weber 1975, Skougard and Brotherson 1979). The anatomy of halophytes and their ecological adaptations to saline soils are also well reviewed (Anderson 1974, Caldwell 1974, Hansen 1974).

Soil salinity is considered to be the most important variable in controlling halophyte distribution (Ungar 1974). However, salinity in combination with other factors has also been shown to be important in controlling the distribution of halophytic species. For example, Hutchinson (1982) showed the importance of salinity and salinity-elevational interactions to account for variations in halophyte distributions. A halophyte is defined as a species which can tolerate levels of salinity greater than 0.5% (Barbour 1970, Chapman 1974). Few species are believed to be obligate halophytes (Ungar et al. 1969, Barbour 1970, Ungar 1974).

Hydrogen ion concentration (pH) has also been suggested as an important determinant of halophyte species distribution (van der Maarel and Leertouwer 1967, Stolfelt 1972, Skougard and Brotherson 1979). Alternatively, pH may not be as closely correlated to biological phenomena since broad overlaps in pH exist between plant communities (Daubenmire 1959a, Ungar et al. 1969).

The relations of moisture in determining species composition and distribution have long been studied. Curtis (1955) discusses the use of indicator species in describing communities with environments of varying moisture content. Dix and Butler (1960) state that moisture is the principle environmental factor controlling species composition in a mesic-dry and dry prairie in Wisconsin. Also, Skougard and Brotherson (1979) discussed the influence of soil moisture as a factor in determining zonation patterns of vascular plants in playa meadows in central Utah. Moisture was noted to be second to salinity in such influence.

Van der Maarel and Leertouwer (1967) determined soil moisture and organic matter to be positively correlated. This is reasonable since an increase in moisture produces an increase in biomass and ultimately more litter and organic matter.

The present study was undertaken to describe patterns of zonation along a slope in a saline meadow and to determine which of several soil factors (texture, salinity, mineral nutrients, etc.) tended to influence that zonation.

STUDY SITE

The study site is located along the west

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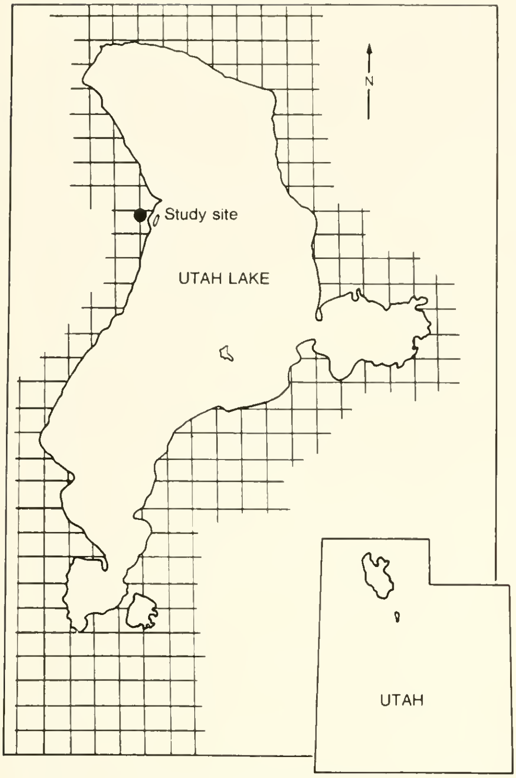

Fig. 1. Map of study site location along west shore of Utah Lake.

shore of Utah Lake at T6S, R1E, S32 (Salt Lake base and meridian), Utah County, Utah, approximately 1.4 km south of Pelican Point (Fig. 1). Zonation within the meadow is visually apparent since different species associations are discretely distributed along a mild slope which parallels the lake. Five zones are distinguishable on the basis of the most obvious species and/or life form: saltgrass–annual weed, saltgrass-alkaligrass, saltgrass-forb, saltgrass, and spikerush (Fig. 2). The first four zones occur along a gradient moving downslope and away from the lake with a vertical drop of 2.5 m. The fifth zone (farthest from the lake) rises approximately 3.0 m.

MATERIALS AND METHODS

Fifteen 5 x 15 m plots (three per zone) were placed along the slope. Each plot was subsampled by 10 quarter-meter-square quadrats. Total living plant cover, plant cover by life form (i.e., perennial forbs, perennial grasses, sedges, rushes, annual grasses, annual forbs), litter, and bare soil were ocularly estimated from each quadrat following a procedure suggested by Ostler et al. (1981). Cover for all plant species encountered was also estimated using the cover-class categories suggested by Daubenmire (1959).

Three soil samples taken in each plot (from opposite corners and the center) from the top 20 cm of soil by means of a tube soil probe were later combined for laboratory analysis. This depth was considered adequate because Christie (1979), with respect to grasslands, found that the top layer of soil is the region of most active mineral uptake. Soil samples were placed in zip-type plastic bags to retain moisture. Percent soil moisture was obtained by weighing fresh soil, drying at 90 C for 72 hours, and reweighing (Skougard and Brotherson 1979).

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition, and organic matter. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 soil-water paste (Russel 1948) was used to determine pH and total soluble salts. Soils were extracted with 1.0 normal neutral ammonium acetate for the analysis of calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils by use of DTPA (diethylenetriamine-penta-acetic acid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted by sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was made using macro-Kjeldahl (Jackson 1958). Organic matter was determined by total carbon measurement via burning 10 g of soil sample at 950 C in a LECO medium temperature resistance furnace following Allison (1965).

Plant nomenclature follows Arnow et al. (1980) for the dicotyledons and Cronquist et al. (1977) for the monocotyledons.

Data analysis consisted of computing means, standard deviations, and coefficients of variation for all measured biotic and abiotic variables (Ott 1977). Correlation coefficients were determined for each combination of all

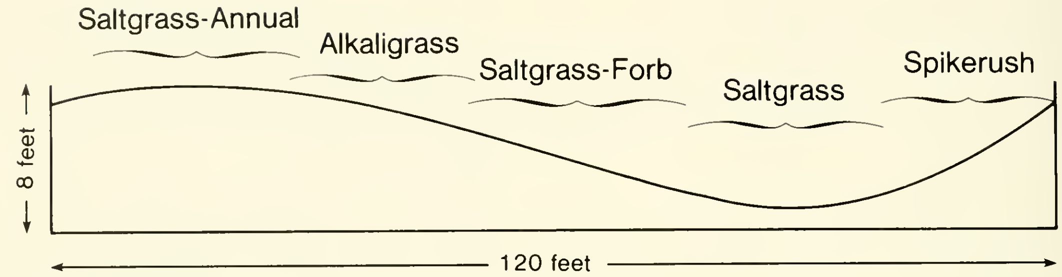

Fig. 2. Graphic representation of slope depicting vegetative zonation patterns on the study site.

TABLE 1. Site factors along with their means and standard deviations found along a slope with respect to vegetation zones in a saline meadow. Zone 1 is saltgrass-annual at the ridge top; Zone 2 is saltgrass-alkaligrass at the slope shoulder; Zone 3 is saltgrass-forb at the slope base; Zone 4 is saltgrass at the slope bottom; and Zone 5 is spikerush (see Fig. 2).

	Zone				
Site factor	1	2	3	4	5
GENERAL SOIL FACTORS:					
Percent sand	10.60	11.73	24.07	34.93	13.07
	±6.70	±5.47	±1.57	±12.03	±3.87
Percent silt	55.00	46.67	47.53	41.10	48.33
	±0.00	±2.89	±12.06	±5.70	±2.89
Percent clay	34.40	±41.60	±28.40	±23.97	±38.60
	±0.70	±8.34	±11.52	±9.45	±6.75
Percent fines	89.40	88.27	75.93	65.07	86.93
	±0.70	±5.47	11.57	±12.03	±3.87
Percent organic matter	17.08	17.59	24.14	24.36	32.70
	±1.10	2.10	±3.73	3.48	16.81
pH	8.70	8.47	7.91	7.73	7.66
	±0.11	±0.14	±0.02	±0.13	±0.11
Soluble salts (ppm)	20,753.33	14,480.67	8,129.00	3,382.67	4,002.67
	±4,646.90	±6,065.71	±711.45	±497.29	±351.48
Soil moisture (%)	25.9	31.1	34.0	39.3	51.7
	±0.67	±2.3	±5.5	±2.5	±3.4
SOIL MINERAL NUTRIENTS:					
Nitrogen (%)	0.142	0.227	0.398	0.585	0.282
	±0.019	±0.041	±0.082	±0.080	±0.123
Phosphorus (%)	15.80	8.0	26.03	27.93	10.13
	±3.06	±1.23	±3.00	±1.42	±4.96
Calcium (ppm)	82,688.00	78,378.67	14,592.00	15,753.33	80,256.00
	±16,566.98	±22,777.65	±1,336.36	±994.23	±8,183.00
Magnesium (ppm)	1,000.00	1,354.67	485.33	757.33	685.33
	±159.3	±52.05	±169.01	±33.31	±110.37
Sodium (ppm)	2,032.00	2,330.67	912.00	1,197.33	1,122.67
	±115.38	±710.03	±120.80	±383.44	±304.56
Potassium (ppm)	893.33	1,005.33	509.33	536.00	576.00
	±92.03	±137.95	±145.40	±188.13	±227.82
Iron (ppm)	1.36	1.41	35.57	62.67	1.84
	±0.08	±.032	±12.04	±40.03	±0.32
Manganese (ppm)	9.35	10.75	10.61	14.92	10.82
	±1.11	±1.82	±2.04	±7.57	±5.74
Zinc (ppm)	1.60	0.92	3.89	4.79	0.62
	±0.25	±0.19	±2.38	±1.67	±0.12
Copper (ppm)	1.60	2.77	4.79	5.94	2.49
	±0.45	±0.64	±1.24	±1.10	±0.68

Table 1 continued.

	Zone				
Site factor	1	2	3	4	5
BIOTIC FACTORS:					
Perennial grass cover (%)	30.6 ±6.7	73.7 ±6.8	43.2 ±10.0	99.0 ±1.6	20.2 ±13.2
Perennial forb cover (%)	14.3 ±3.2	0.6 ±0.6	48.1 ±13.3	0.0 ±0.0	20.1 ±4.8
Sedge cover (%)	0.0 ±0.0	0.1 ±0.0	6.4 ±4.5	0.1 ±0.0	11.1 ±1.4
Rush cover (%)	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0	0.9 ±1.5	47.1 ±15.8
Annual forb cover (%)	55.8 ±7.6	25.7 ±7.3	0.8 ±1.2	0.1 ±0.0	0.1 ±0.0
Mean number of species/stand	5.00 ±0.00	9.00 ±1.73	10.33 ±1.53	2.67 ±1.53	8.00 ±1.00
Mean number of native species/stand	3.00 ±0.00	7.00 ±1.00	8.67 ±1.53	2.67 ±1.53	6.67 ±0.58
Mean number/ introduced species/stand	2.00 ±0.00	2.00 ±1.00	1.67 ±0.58	0.0 ±0.0	1.33 ±0.58
Native species (% of total no.)	60.00 ±0.0	78.67 ±8.08	83.67 ±6.03	100.00 ±0.00	84.00 ±5.29
Introduced species (% of total no.)	40.00 ±0.0	21.33 ±8.08	16.33 ±6.03	0.00 ±0.00	16.00 ±5.29
Species diversity	1.51	1.35	1.78	0.06	1.57
PERCENT COVER:					
Native species	55.67 ±17.21	97.33 ±1.53	92.00 ±12.17	100.00 ±0.0	81.33 ±7.02
Introduced species	44.33 ±17.21	2.67 ±1.53	8.00 ±12.17	0.00 ±0.00	18.67 ±7.02

site parameters (Cochran and Snedecor 1976). Species diversity was determined based on cover values using Shannon-Weaver's index of diversity (Kempton and Reddenburn 1978).

RESULTS AND DISCUSSION

Results of the soil analyses are given in Table 1. Several patterns of change along the downslope gradient can be observed. For example: (1) organic matter and percent soil moisture increase; (2) pH decreases; (3) silt, fines, and soluble salts decrease to the saltgrass zone and then increase in the spikerush zone; (4) sand, nitrogen, and copper increase to the saltgrass zone and then decrease in the spikerush zone; (5) magnesium, sodium, and potassium are high in the saltgrass–annual weed and saltgrass-alkaligrass zones and low in the other three zones; (6) phosphorus, iron, and zinc are low in the saltgrass–annual weed and saltgrass-alkaligrass zones, very high in the saltgrass-forb and saltgrass zones, and then low again in the spikerush zone; and (7) calcium is very high in the saltgrass–annual weed and saltgrass-alkaligrass zones, low in the saltgrass-forb and saltgrass zones, and then high again in the spikerush zone. Clay and manganese showed little or no patterns. Although it is not the lowest elevational point of the gradient, the spikerush zone has the highest percent soil moisture levels of any of the zones. This is because the zone overlies seep areas that provide a constant supply of moisture to the surface.

Decreasing salinity downslope could be caused by two factors and/or their interactions. First, water will drain from the high point in the saltgrass–annual weed zone to the lower saltgrass zone. Also, during years of high moisture, the lower elevation areas are seasonally flooded because of lake fluctuations. Increased moisture in the soil will increase the leaching effect on salts (Waisel

TABLE 2. Species and their average percent cover as found in the five vegetative zones of the saline meadow. Zone 1 is at the ridge top and Zone 4 is at the slope bottom. Zone 5 is upslope from Zone 4 overlying a seep area (see Fig. 2).

	Zone				
Species	1	2	3	4	5
Distichlis spicata	31.17	41.52	44.49	99.07	18.25
Kochia scoparia	16.04	0.31			
Lepidium perfoliatum	29.66	0.07	0.39		
Suaeda depressa	9.25	8.85	0.29		
Cressa truxillensis	13.88	0.11			
Puccinellia airoides		32.91			
Salicornia rubra		14.15			
Iva axillaris		0.07	9.71		3.15
Circium undulatum		0.07	0.85		
Triglochin maritima		0.22	10.33		
Polypogon monspeliensis		0.02	0.03		
Juncus balticus		0.02	6.12	0.04	9.79
Sporobolus airoides			0.69		
Glaux maritima			9.41		17.23
Crepis runcinata			13.04		0.60
Asclepias speciosa			0.99		
Ambrosia psilostachya			3.29		
Hordeum jubatum			0.06		0.97
Aster pauciflorus			0.29		0.39
Eleocharis palustris				0.81	47.94
Eleocharis rostellata					0.61
Agropyron repens					1.51

1972). Second, as a soil dries, moisture, together with its dissolved salts, is drawn from the deeper soils. As a result of this "wicking action," water evaporating from the soil surface leaves increased concentrations of dissolved salt in the upper horizon (Waisel 1972, Walter 1973). Consequently, salinity increases along the ridge and decreases in the depression. Any increased salinity in the spikerush zone over the saltgrass zone would be due to this same wicking action of evaporating water since the spikerush area overlies a large seep where water is continuously rising to the surface, evaporating, and leaving its salts behind.

Cover values (Table 2) showed that, with the exception of a few species, saltgrass (*Distichlis spicata*) contributed a major proportion of the plant biomass in each zone. A broad ecological tolerance is not uncommon for saltgrass. Several studies indicate that saltgrass tolerates salinities ranging from 0.03 to 5.4% with an optimum of approximately 1.5% (Ungar 1966, Ungar 1974, Hansen et al. 1976, Skougard and Brotherson 1979). However, where saltgrass was the most lush on our sites, salinity levels were only 0.33%. This agrees with Ungar and McClelland (1969), who found saltgrass growing in a dwarfed state in highly saline soils but very lush when salinity was lower.

Saltgrass has also been shown to grow across a broad range of pH (Hansen et al. 1974, Ungar 1974, Hansen and Weber 1975, Skougard and Brotherson 1979). Ungar (1974) indicates that pH in saltgrass areas generally ranges between 7.5 and 8.5 but may range from 6.8 to 9.2. This corresponds well with our data wherein saltgrass was found growing at pH levels ranging from 7.6 to 8.7. It has been documented that an increase of water in the soil will in effect raise the pH (Russel 1961). This would indicate that if the measured hydrogen ion concentration decreased slowly with increasing soil moisture, the total hydrogen ion concentration may hold relatively constant. If this is the case, the variation in saltgrass cover on our sites is probably not related to changing pH conditions but to other factors.

Correlation analyses between cover of saltgrass and different soil factors (Table 3) further explain the above-mentioned relationships. Saltgrass cover showed positive correlation ($p \leq 0.03$) to elevated levels of sand, nitrogen, iron, zinc, and copper in the soil. It was negatively correlated ($p \leq 0.02$) with soil fines, forb cover, sedge cover, and introduced species cover. The lack of significant correlation to either soluble salts or soil moisture is easily understood in relation to the presence of elevated levels of spikerush cover in Zone 5. Saltgrass cover increases steadily downslope and then decreases dramatically in the spikerush zone, whereas soil moisture increases steadily across all five zones and soluble salts decrease across all five zones. The dramatic increase in spikerush cover and the corresponding decrease in saltgrass cover in the spikerush zone alter the general direction of the saltgrass curve, thus neutralizing the observed trends and therefore the correlation. The role of the mineral nutrients in the distribution of saltgrass is not well understood and needs further study.

Ungar (1974) discussed halophyte zones and associated species. He states that alkaligrass (*Puccinellia airoides*) zones are commonly associated with samphire (*Salicornia rubra*), Pursh seepweed (*Suaeda depressa*), and arrowgrass (*Triglochi maritima*), with samphire and Pursh seepweed generally contributing fair amounts of cover to the community and arrowgrass making up 2% or less of the cover. He also reports soil salinity levels to be between 1.8 and 2.8%, which is considerably higher than shown in our study. Otherwise, the associations found in our meadow are consistent with those of Ungar.

Percent cover by life form is listed for each zone in Table 1. Annual forb cover is highest on the ridge top and then decreases dramatically downslope. Sedge and rush cover are restricted to the wet end of the gradient and show their greatest cover in the spikerush zone. Grass cover spans the total width of the gradient, showing varying degrees of development depending on the zone. Perennial forbs are generally restricted to the saltgrass-forb and spikerush zones but reach their greatest development in the saltgrass-forb zone.

The annual forbs that dominate the ridge top (saltgrass-annual zone) do so because of the dwarfed state of growth in saltgrass, which leaves openings between individual plants where seedlings of species adapted to the more xeric conditions can establish. In addition, they germinate, mature vegetatively, flower, and set seed early in the season when environmental conditions are adequate and before the severe drought of late summer.

The distribution of the perennial forbs along the gradient is of interest. Previously forbs have been shown to occupy wetter habitats than do grasses (Hironaka 1963, Harner and Harper 1973, Yake and Brotherson 1979). Harner and Harper (1973) suggest that this is due to the growth morphology of grasses and forbs; grass stems depend upon cellulose for support, whereas forbs use turgor pressure to support cells. However, our correlations of percent forbs with percent moisture showed no significant relationships. In fact, the perennial forbs in our study showed a bimodal pattern of distribution with their greatest importance being at the wet end of the gradient and a lesser peak at the dry end of the gradient (Table 1). The peak at the ridge top is due to a single species, cressa (*Cressa truxillensis*), whereas the peak in Zone 3 (saltgrass-forb) is due to eight species and the peak in the spikerush zone is due to four species. The total lack of forbs in Zone 4 (saltgrass) and their diminished importance in Zone 5 (spikerush) is best explained by competition. The wetter zones are heavily dominated by saltgrass, common spikerush (*Eleocharis palustris*), sea milkwort (*Glaux maritima*), and wiregrass (*Juncus balticus*), all of which form dense rhizome systems in the upper layer of soil, thus increasing the competition for space and therefore reducing the probability of annual or perennial forbs establishing in those zones.

A second explanation for the high level of perennial forbs in Zone 3 (saltgrass-forb) could be that of mineral nutrition. It is well known that the presence or absence of particular ions in the soil can affect the growth of a plant and thereby profoundly influence its distribution (Jefferies et al. 1968). For example, fertilizing with nitrogen and phosphorus was found to influence the distribution of salt marsh forbs (Pigott 1968). Also, Thurston (1968) found that the addition of phosphorus, potassium, sodium, and magnesium to native pastures in England altered the distribution of forb species belonging to the Fabaceae. The presence of high levels of phosphorus, iron, zinc, copper, and nitrogen in the soils of Zone 3 could indicate nutrient conditions in the soil which favor the growth and establishment of the perennial forbs. However, further research must be done to fully answer these questions.

The distribution of introduced species in the meadow was positively correlated with

TABLE 3. Results of correlation analysis between site factors (biotic and abiotic) associated with five vegetation zones in the saline meadow.

Environmental variable	Positive correlations	Negative correlations
Soil moisture (%)	Organic matter (0.0001) Sedge cover (0.0001)	pH (0.0002) Soluble salts (0.002) Sodium (0.03)
Organic matter (%)	Soil moisture (0.0001) Sedge cover (0.0002)	pH (0.0002) Soluble salts (0.01)
Soluble salts (ppm)	Calcium (0.03) Fines (0.03) Magnesium (0.02) Number of introduced species/stand (0.004) pH (0.0001) Potassium (0.005) Sodium (0.03)	Copper (0.03) Nitrogen (0.01) Soil moisture (0.002) Soil organic matter (0.01) Sand (0.03)
pH	Calcium (0.03) Fines (0.03) Magnesium (0.004) Number of introduced species/stand (0.01) Potassium (0.002) Soluble salts (0.0001) Sodium (0.004)	Copper (0.04) Nitrogen (0.005) Soil moisture (0.0002) Soil organic matter (0.0002) Sedge cover (0.02) Sand (0.03)
Sand (%)	Copper (0.004) Saltgrass cover (0.02) Iron (0.02) Nitrogen (0.0001) Grass cover (0.02) Phosphorus (0.02) Zinc (0.01)	Calcium (0.0003) Clay (0.0006) Fines (0.0001) Number of introduced species/stand (0.004) Forb cover (0.01) pH (0.03) Potassium (0.04) Soluble salts (0.03)
Silt (%)	Introduced species cover (0.02) Number of introduced species/stand (0.004) Forb cover (0.01)	Copper (0.02) Nitrogen (0.05) Grass cover (0.04) Zinc (0.02)
Clay (%)	Calcium (0.07) Fines (0.0006)	Phosphorus (0.01) Sand (0.006)
Fines (%)	Calcium (0.0003) Clay (0.0006) Number of introduced species/stand (0.004) Forb cover (0.01) pH (0.03) Potassium (0.04) Soluble salts (0.03)	Copper (0.004) Saltgrass cover (0.02) Iron (0.02) Nitrogen (0.0001) Grass cover (0.02) Phosphorus (0.001) Sand (0.0001) Zinc (0.01)
Nitrogen (ppm)	Copper (0.0001) Saltgrass cover (0.03) Iron (0.004) Grass cover (0.01) Phosphorus (0.0007) Sand (0.0001) Zinc (0.0003)	Calcium (0.001) Fines (0.0001) Introduced species cover (0.008) Number of introduced species/stand (0.002) Forb cover (0.005) pH (0.005) Potassium (0.02) Soluble salts (0.01) Silt (0.005) Sodium (0.04)

Table 3 continued.

Environmental variable	Positive correlations	Negative correlations
Phosphorus (ppm)	Copper (0.0003) Iron (0.0006) Nitrogen (0.0007) Sand (0.001) Zinc (0.0002)	Calcium (0.0001) Clay (0.01) Fines (0.001) Magnesium (0.04) Number of introduced species/stand (0.04) Potassium (0.05) Sodium (0.05)
Calcium (ppm)	Clay (0.007) Fines (0.0003) Magnesium (0.01) Number of introduced species/stand (0.02) pH (0.03) Potassium (0.01) Soluble salts (0.03)	Copper (0.0008) Iron (0.001) Nitrogen (0.001) Phosphorus (0.0001) Sand (0.0003) Zinc (0.0005)
Magnesium (ppm)	Calcium (0.01) pH (0.004) Potassium (0.0001) Soluble salts (0.02)	Phosphorus (0.04)
Sodium (ppm)	Magnesium (0.0003) pH (0.004) Potassium (0.0002) Soluble salts (0.03)	Copper (0.04) Nitrogen (0.04) Soil moisture (0.03) Phosphorus (0.05)
Potassium (ppm)	Calcium (0.01) Fines (0.04) Magnesium (0.0001) Number of introduced species/stand (0.05) pH (0.002) Soluble salts (0.005) Sodium (0.0002)	Nitrogen (0.02) Phosphorus (0.05) Sand (0.04)
Iron (ppm)	Copper (0.0001) Saltgrass cover (0.03) Manganese (0.02) Nitrogen (0.004) Grass cover (0.03) Phosphorus (0.0006) Sand (0.02) Zinc (0.0001)	Calcium (0.001) Fines (0.02) Number of introduced species/stand (0.01) Forb cover (0.02)
Manganese (ppm)	Copper (0.03) Iron (0.02)	
Zinc (ppm)	Copper (0.0001) Saltgrass cover (0.03) Iron (0.0001) Nitrogen (0.0003) Grass cover (0.03) Phosphorus (0.0002) Sand (0.01)	Calcium (0.0005) Fines (0.01) Introduced species cover (0.05) Number of introduced species/stand (0.02) Forb cover (0.02) Silt (0.02)
Copper (ppm)	Saltgrass cover (0.02) Iron (0.0001) Manganese (0.03) Nitrogen (0.0001) Grass cover (0.01) Phosphorus (0.0003) Sand (0.004)	Calcium (0.0008) Fines (0.004) Introduced species cover (0.0007) Number of introduced species/stand (0.01) Forb cover (0.004)

Table 3 continued.

Environmental variable	Positive correlations	Negative correlations
	Zinc (0.0001)	pH (0.04) Soluble salts (0.03) Silt (0.02) Sodium (0.04)
Grass cover (%)	Copper (0.01) Saltgrass cover (0.0001) Iron (0.03) Nitrogen (0.01) Sand (0.02) Zinc (0.03)	Fines (0.02) Introduced species cover (0.009) Forb cover (0.0001) Sedge cover (0.03) Silt (0.04)
Annual forb cover (%)	Soluble salts (0.001) pH (0.001) Silt (0.05) Fines (0.05) Calcium (0.05) Magnesium (0.05) Sodium (0.01) Potassium (0.01) Introduced species cover (0.01)	Soil moisture (0.01) Organic matter (0.01) Sand (0.05) Nitrogen (0.01) Zinc (0.01) Sedges (0.05)
Perennial forb cover (%)	Species diversity (0.05)	Saltgrass (0.05) Magnesium (0.05) Sodium (0.05) Grass cover (0.03) Potassium (0.05)
Sedge cover (%)	Soil moisture (0.0001) Soil organic matter (0.0002)	Saltgrass cover (0.008) Grass cover (0.03) pH (0.02)
Introduced species cover (%)	Fines (0.002) Silt (0.02)	Copper (0.007) Saltgrass cover (0.02) Nitrogen (0.008) Grass cover (0.009) Zinc (0.005)
Number of introduced species/stand	Calcium (0.002) Fines (0.004) pH (0.01) Potassium (0.05) Soluble salts (0.004) Silt (0.04)	Copper (0.01) Iron (0.01) Nitrogen (0.002) Phosphorus (0.04) Sand (0.004) Zinc (0.02)
Saltgrass cover (%)	Copper (0.01) Iron (0.03) Nitrogen (0.03) Grass cover (0.0001) Sand (0.02) Zinc (0.003)	Fines (0.02) Introduced species cover (0.02) Forb cover (0.0001) Sedge cover (0.008)

silt, fines, pH, soluble salts, calcium, and potassium (Table 3). In all cases these factors increase from slope base to ridge top. Since the highest importance of the introduced species was at the ridge top, as were the above-mentioned factors, the correlations are explainable. However, cause and effect may not necessarily be involved because the role of competition from other species and open habitat availability have not been measured. It is clear that saltgrass grows in a dwarfed and less-dense state at the ridge top (Table 2), and so competition should be reduced and habitat availability for the introduced annual species enhanced.

Species diversity for each zone is reported in Table 1. Correlation analysis between species diversity and perennial forb cover (Table 3) showed that a positive association developed, indicating that patterns of forb distribution influence diversity in the meadow.

Correlation coefficients for each possible pair of independent variables are given in Table 3. All correlations listed are significant ($p \leq 0.05$). As shown, there is a high number of significant correlations among factors. A careful review of the data indicates that the majority of the correlations in some way reflect the gradually changing conditions of environment associated with slope position. When this is understood and we examine the relationships of vegetation to slope position, it is possible to see trends.

Annual forbs occupy the more xeric sites along the ridge top where the soils are fine textured and soluble salts and pH are high. The dry-site annuals appear to do well in this zone partly because of the dwarfed and less-dense growth habit of saltgrass. This growth pattern would allow for reduced interspecific competition between the grass and the annuals. Alternatively, sedges and rushes occupy the wet end of the gradient where the soils are less finely textured and are lower in soluble salts and pH. Underlying springs and seeps keep this end of the gradient moist. The perennial forbs become dominant in Zone 3 at the base of the slope where several of the soil nutrients peak and where soil moisture, soluble salts, and pH levels are moderate. Grasses vary widely across the full extent of the gradient, showing peaks in Zones 2 and 4. Correlation analysis showed the high levels of grass cover to be positively associated with elevated levels of micronutrients, nitrogen, and sand. The roles of soil salinity, pH, and moisture are not as clearly defined as in other cases (Ungar 1974, Skougard and Brotherson 1979) because of the uniform way they vary in relationship to the slope gradient and to each other. The slope acts as a vehicle wherein the different soil parameters become highly integrated into an environment that varies continuously and thus masks the influence of a single factor on the vegetation patterns. Similar conditions were found in a brackish marsh in Canada where an elevation/salinity/soil texture and soil water content interaction was shown to be responsible for species distribution patterns (Hutchinson 1982).

Saltgrass was present in all five zones; few other species extended themselves into multiple zones (Table 2). The distribution of the different species along the slope gradient generally approximated the classical bell-shaped curves so reminiscent of Curtis' (1955) vegetational continuum theory. This indicates that the distribution of the species along the slope cannot easily be accounted for by one or two variables, but that competition, soil moisture, soil chemistry and texture, soil minerals, and vertebrate and invertebrate relations all play a role. In this regard the distribution of some species will be primarily related to one factor, while other species distribution will be controlled by a different set of factors. However, since there is such a high degree of correlation between the majority of soil factors, the overall zonation patterns in the vegetation can best be understood when thought of as reflecting the underlying patterns of the abiotic and biotic environment.

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AGE IN RELATIONSHIP TO STEM CIRCUMFERENCE AND STEM DIAMETER IN CLIFFROSE (*COWANIA MEXICANA* VAR. *STANSBURIANA*) IN CENTRAL UTAH

J. D. Brotherson[1], K. P. Price[2], and L. O'Rourke[1]

ABSTRACT.—Cliffrose age in relation to stem circumference and stem diameter was studied in central Utah. Age-circumference and age-diameter predictor equations were developed from material obtained from 10 stands along a 65-km section of the Wasatch Mountains foothills. Ages estimated on material of known age by the two equations were highly similar. Age predictions were more accurate for young stems than for older stems. The oldest stem aged was 163 years.

Population biology seeks to understand and interpret variations in the numbers of organisms as they are distributed in time and space. Among the populations of a given species, differences in size of individuals, density, age structure, and morphological characters often reflect underlying variations in the genetics of those populations as well as the way in which they interact, survive, and reproduce in their individual environments. Successful reproduction in a species over ecological and evolutionary time and across a range of environments, combined with the development of wide variation in the attributes of its individual populations, is of interest. Measurement of population size, density, age structure, and morphological variation is enhanced when a reliable tool for aging the individuals of a population can be employed.

Studies of growth-ring variation in tree populations have been used extensively for dating (Douglas 1935, Glock 1937), reconstruction of past climates (Fruits 1971, Harper 1979), interpretation of successional dynamics (Burkhardt and Tisdale 1969, Barney 1972), and assessment of differences in the environments of selected habitats (Ferguson and Humphrey 1959, Fritts 1962, Stockton and Fritts 1973). Although trees have been the primary focus of such studies, papers dealing with habitat variations and age-prediction models for shrubs are available (Ferguson 1958, Ferguson and Humphrey 1959, Brotherson et al. 1980, Brotherson et al. 1984). Studies dealing with circumference-age relationships of shrubs and their value in the development of age-prediction models, interpretations of habitat factor differences, and successional dynamics are less known. Many western shrub species show asymmetrical stem growth; this suggests the need to understand the relationship between stem circumference and age for studies in population dynamics. This study considers stem diameter and stem circumference–age relationships of cliffrose (*Cowania mexicana* var. *stansburiana*) from sites in central Utah.

STUDY AREA

The study area is located along the gravelly shores of prehistoric Lake Bonneville on the west face of the Wasatch Mountains, Utah County, Utah, between American Fork Canyon on the north and Santaquin Canyon on the south, a distance of 65 km. Elevation varied little across the sites, averaging 1,562 m. Aspect varied between 140 and 330 degrees on a standard compass bearing. The cliffrose populations selected for study were chosen from the largest and most dense stands in the area. Soils, which varied from gravelly sandy loams to gravelly clay loams, were heavily skeletal (Price and Brotherson 1987), slightly basic (pH = 7.7), and very low in soluble salts. Soil mineral nutrient concentrations were also very low (Price and Brotherson 1987).

The Wasatch Mountains are primarily composed of sedimentary limestone formations

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TABLE 1. Predictor equations for cliffrose age along with deviations of estimated age from true age for stems of known material.

Estimator factor	Prediction equation	r^2	Sig. level	Deviation of estimated age from true age		
				$\bar{x}$	SD	CV
Diameter	$\hat{y} = 6.801 + 14.209x$	0.69	0.001	5.8	4.8	1.2
Circumference	$\hat{y} = 5.450 + 4.728x$	0.73	0.001	6.1	5.1	1.2

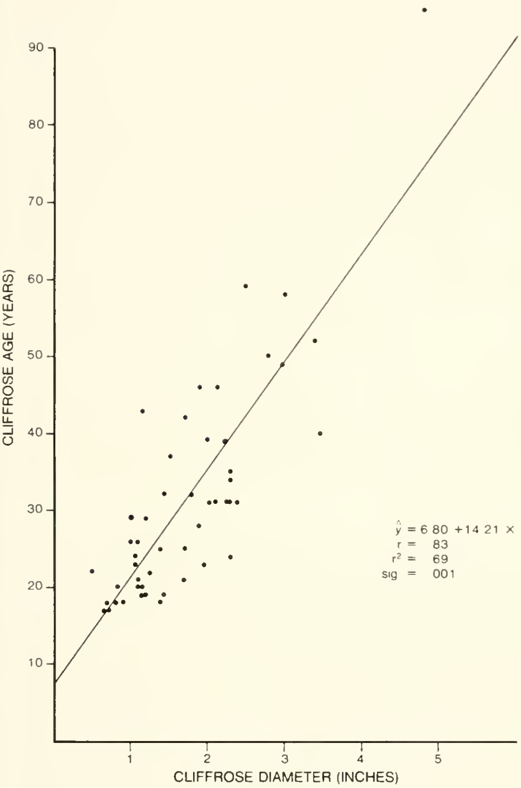

Fig. 1. The relationship between stem diameter and stem age in cliffrose in central Utah.

high in calcium carbonate. Rainfall in the area averages 422 mm (NOAA 1922–72), with approximately 280 mm falling between October and April (USDA 1972). The average annual temperature is 10.6 C, with a frost-free period averaging 150 days.

Cliffrose, rubber rabbitbrush (*Chrysothamnus nauseosus*), and *Artemisia tridentata* dominated the site overstory. The understory was dominated by annuals of which cheatgrass (*Bromus tectorum*), madwort (*Alyssum alyssoides*), Japanese brome (*Bromus japonicus*), tumblemustard (*Sisymbrium altissimum*), and cutleaf filaree (*Erodium cicutarium*) were the most important. The perennial bluebunch wheatgrass (*Agropyron spicatum*) was also important in the understory (Price and Brotherson 1987).

METHODS

Ten study sites, each 10 x 10 m (0.01 ha), were selected from the above communities. Five stems, each from randomly selected individuals, were obtained from the 10 sites for a total of 50 stems. Stems were sectioned diagonally, polished with fine sandpaper, and the annual growth rings counted twice (independently) at the widest part of the stem with the aid of a stereoscopic microscope (Ferguson 1970, Brotherson et al. 1980). One ring was assumed to equal one year of growth. Stem diameters and circumferences were measured with a diameter tape.

Linear regressions of age on diameter and age on circumference generated stem diameter–age and stem circumference–age predictor equations (Brotherson et al. 1980). The predictor equations were then checked by estimating the stems of known age. The predictor equations were also used to predict mean ages of the 10 populations.

RESULTS AND DISCUSSION

Cliffrose in central Utah generally grows on escarpments with southwest exposures having greater than 40% slope. The populations studied in this report were located along what had once been the gravelly shoreline of old Lake Bonneville. Adjacent, finer-textured soils that accumulated on the bottom of the lake apparently create a barrier to the species, confining it to the better-drained, lighter-textured soils of the ancient beach. The sites are typically exposed to environmental severities and are subject to wide variations in environmental extremes. Successful inhabitants of these sites must withstand a broad range of environmental fluctuations. Often such envi-

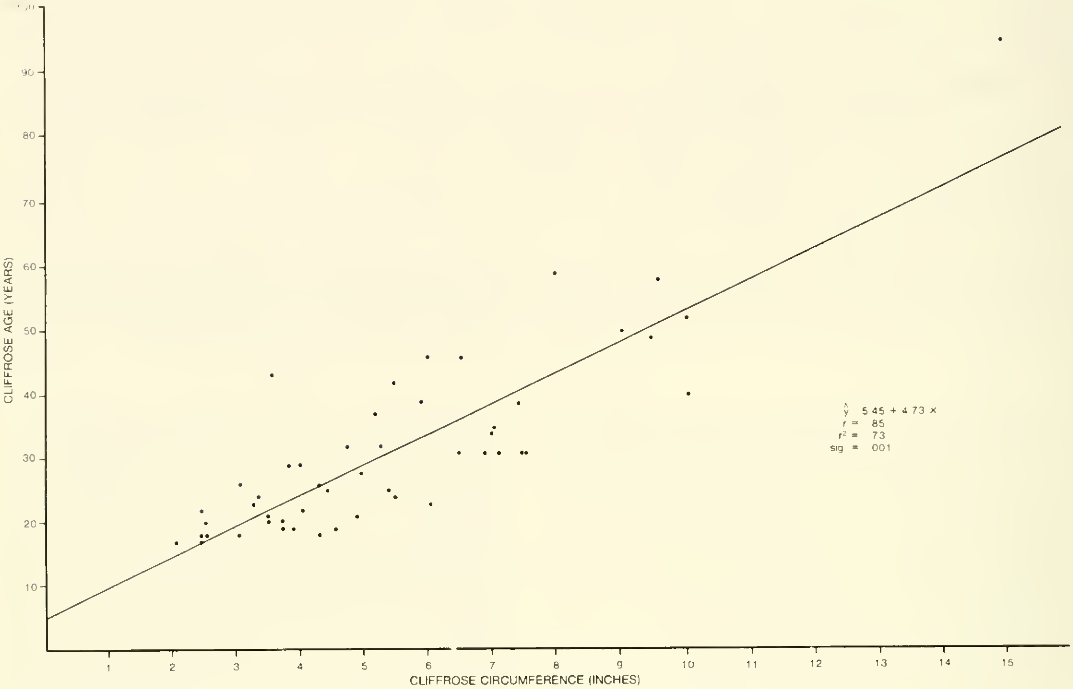

Fig. 2. The relationship between stem circumference and stem age in cliffrose in central Utah.

ronmental variation is evidenced in differential growth rates, varying plant heights, and morphology of individuals of separate populations. Such was the case with respect to our 10 populations. For example, average length of annual twig growth varied across these populations from a low of 2.0 cm to a high of 13.3 cm, indicating variable growth rates between the different populations.

Cliffrose stem diameters ranged from 0.5 inches to 4.8 inches, and the circumferences varied from 2.44 inches to 15.06 inches. Linear regression was used to establish age-diameter ($r^2 = 0.69$) and age-circumference ($r^2 = 0.73$) predictor equations (Table 1, Figs. 1 and 2). Both equations were significant at the 0.001 level. The slightly better fit of the circumference equation is due to the irregular growth patterns of the cliffrose stems. This irregular growth form (asymmetrical) made it very difficult to measure the stem diameters, especially under field conditions. The diameters were measured at the widest part of the stem.

When the two predictor equations were used to estimate stem ages from original material (stems used to generate the equations), the estimated ages showed no significant difference (Table 1). The diameter-age predictor equation estimated the ages more accurately than did the circumference-age predictor equation. However, there were no significant differences between true age and estimated age. Stem diameter and stem circumference were plotted against one another (Fig. 3). The relationship is significant ($p \leq 0.001$; $r^2 = 0.98$), indicating that either diameter or circumference may be used to determine the age of cliffrose in this area. However, circumference measurements may be more accurately obtained in the field because of the irregular growth patterns of the cliffrose stems.

Results indicate that the predictor equations are more accurate for young stem age than for older stem age (Fig. 4). When the deviation of predicted age from true age is plotted against true age, the difference increases as cliffrose stems get older. Similarly, as the stems of mountain mahogany (*Cercocarpus*) get older, they grow slower and show smaller widths in their growth rings (Brotherson et al. 1980).

Basal circumference measurements were taken on 30 randomly selected individuals per

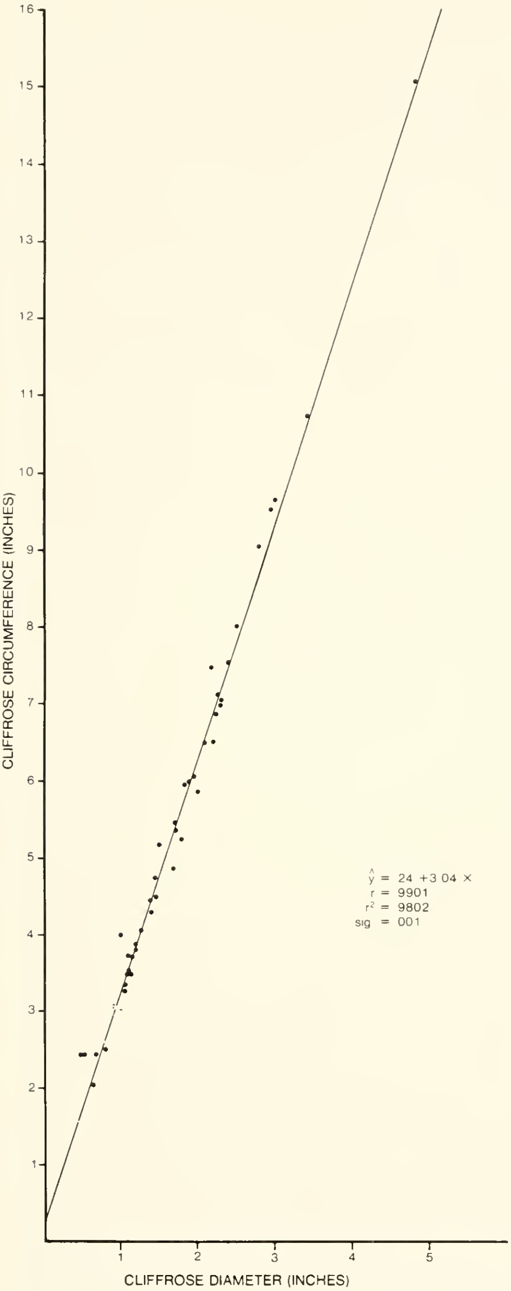

Fig. 3. The relationship between stem diameter and stem circumference in cliffrose in central Utah.

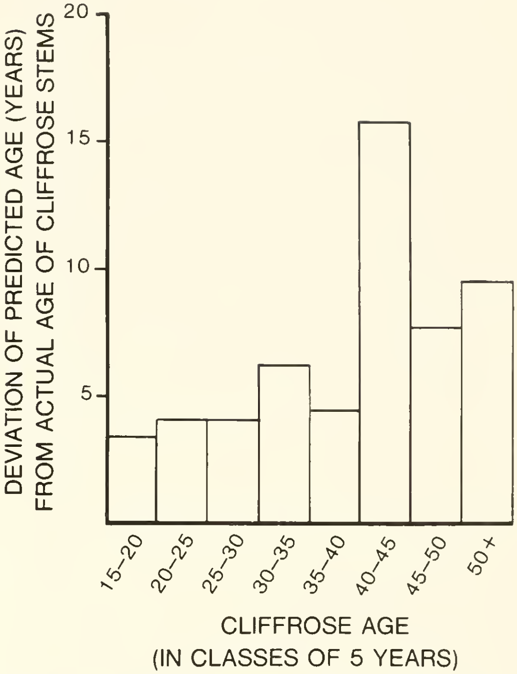

Fig. 4. The relationship of the difference between predicted age and true age in cliffrose in central Utah.

site for 9 of the 10 sites. One site had only 18 living individuals. From these basal measurements (288 individuals), the plants of each stand were aged. The youngest individual found was 11 years old and the oldest 163 years. When the ages for all individuals of a specific site were averaged, the youngest population was 28 years and the oldest 69 years. Average community age was found to be negatively correlated with cliffrose density ($p \leq 0.05$) and positively with a hedging index ($p \leq 0.001$), indicating that the longer the population has been established, the taller and less dense the individuals become. This, we feel, is due to the impact of wildlife (specifically mule deer) on cliffrose plants, since they are preferred forage for these animals.

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DEMOGRAPHY OF BLACK-TAILED PRAIRIE DOG POPULATIONS REOCCUPYING SITES TREATED WITH RODENTICIDE

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Abstract.—A rodenticide, zinc phosphide, was applied to remove black-tailed prairie dogs (*Cynomys ludovicianus*) from 6 ha of a prairie dog colony in southwestern South Dakota. Another adjacent 6 ha was left untreated. The removal experiment was repeated two consecutive years. Contingency table analysis showed that the resultant population was not homogeneous; age classes by sex of the immigrant and resident subpopulations were different ($P < 0.01$). The ratio of adult females to yearling females was greater among immigrants than among residents ($P < 0.03$). Female immigrants did not produce young in the treated zone during the year of their arrival. Fewer of these females displayed distended nipples than expected ($P < 0.01$), indicating that these immigrants did not reproduce during the reproductive season immediately preceding dispersal and suggesting that failure to reproduce may have stimulated dispersal.

The black-tailed prairie dog (*Cynomys ludovicianus*) is a herbivorous, social ground squirrel that is native to the Great Plains of North America. Black-tailed prairie dogs live in colonies known as prairie dog towns. Within these colonies, prairie dogs dig burrows and alter the composition of the vegetation (Koford 1958, Coppock et al. 1983). Large populations of black-tailed prairie dogs presently exist within the boundaries of Badlands National Park, South Dakota.

During the 10 years prior to this study, prairie dog towns had expanded in the park and on other federal, state, and private rangeland and farmland (Schenbeck 1982). Managers of parks and refuges sought to reduce the black-tailed prairie dog populations by applying rodenticides to diminish conflicts with rangeland users beyond their boundaries. However, this practice has not always been cost-effective (Collins et al. 1984). The rapid invasion of treated colonies by other immigrating prairie dogs is a major cause of failure of prairie dog control. If a source of immigrants is present, black-tailed prairie dogs can regain their initial population numbers within 1 to 3 years following the application of rodenticide to the town (Knowles 1985). Elimination of immigrant individuals that take up residence in vacant burrows of the treated colony must be accomplished before control programs can be successful. Information is needed that can identify the origin, demography, and behavior of prairie dogs that reinhabit a colony after application of rodenticides. Our study focused on the demography of immigrant populations of black-tailed prairie dogs that formed after rodenticide treatment of the original population. The objective in this study was to determine differences in sex and age-class distributions between resident and immigrant populations.

Study Area and Methods

The study was conducted during three summer field seasons from 1981 to 1983 on a colony northwest of the edge of the Robert's prairie dog town in Badlands National Park, southwestern South Dakota. The area received approximately 40 cm of precipitation annually, most of which fell between early April and mid-July during intense, patchy thunderstorms. The mean temperature was 10 C, ranging from −5 C in January to 26 C in July.

Soils in the study area were deep, sandy-loam sediments interspersed with thin layers of sand and gravel from former stream beds. Topography of the area was gently rolling, mixed-grass prairie. Dominant plant species were western wheatgrass (*Agropyron smithii*), buffalograss (*Buchloe dactyloides*), needle-and-thread grass (*Stipa comata*), blue grama (*Bouteloua gracilis*), Patagonia Indian-wheat (*Plantago patagonica*), and prostrate vervain (*Verbena bracteata*).

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A 12-ha segment of the colony that bordered uncolonized grassland was used. The northern 6 ha of the site was chosen for rodenticide treatment; the remaining 6 ha was left untreated. Since black-tailed prairie dogs are highly territorial, rarely leaving the boundaries of their territories to forage (King 1955), the treated and untreated zones were purposefully set out adjacently to determine if individuals from the untreated half would abandon their territories to occupy the nearby vacant burrows or expand their territories into the treated side of the colony. We trapped the population on this site before beginning treatment to determine the original demography of the resident colony and to test for heterogeneity of the population due only to the location of the zones proposed to be treated or left untreated. Rodenticide (2% zinc phosphide coated grain) was applied to the treated 6 ha after pretreatment grain was applied according to published recommendations (Tietjan 1976). Rodenticide was placed on all burrow mounds during the last week of August 1981 and 1982. The control site was left untreated. Thus, population samples of prairie dogs in the treated zone in both 1982 and 1983 were newly arrived immigrants, while a continuous population of residents was concurrently monitored in the untreated zone.

All prairie dogs were trapped and marked during the first week in June and third week in August 1982 and 1983. We trapped in two sessions to avoid missing individuals that were difficult to trap or had not yet immigrated. Prairie dogs were trapped using 52 Tomahawk 32-inch live-traps (no. 206) baited with commercial sweet chop, a molasses-coated mixture of cracked corn, rolled barley, and rolled oats. All animals were toe-clipped for identification and then released. Prairie dogs were classed as adults (> 1 yr), yearlings, or juveniles, based upon their condition, size, weight, and previous record of capture.

We addressed differences between immigrants and residents with the null hypothesis that the resulting population was demographically undisturbed by treatment and immigration; we expected the population to be homogeneous. Observed sex ratios, the distribution of age classes by sex, and adult to yearling ratios by sex of the newly arrived immigrant subpopulation were tested against the distribution of the untreated, continuously growing subpopulation in contingency tables with fixed-row and column values. Expected cell frequencies were generated and assumed to be the expected discrete distribution for test of population homogeneity using the chi-square statistic ($\alpha = 0.05$). An analysis was performed separately for 1982 and 1983 observed populations. The chi-square statistic was used, as well, to determine significance of *a posteriori* differences observed between the immigrants and residents.

Though an intensive effort was mounted to trap all individuals by selectively situating traps, it became obvious that some animals were not captured. We assumed that this untrapped portion of the population was small and not confined to any particular age class or sex. We also assumed that marking and trapping of the animals did not influence their dispersal behavior.

RESULTS AND DISCUSSION

Before zinc phosphide was applied, a total of 76 individuals were captured during summer 1981 (Table 1) in the zone reserved for future rodenticide treatment. Only 55 prairie dogs were captured during the same period in the adjacent part of the colony, which would remain untreated. This population was statistically homogeneous, though there were noteworthy differences between the spatially segregated subpopulations that were not statistically significant at the chosen alpha-level. The population sex ratio in the future treated zone was 1.30:1, and that observed in the future untreated zone was 0.72:1 ($X^2 = 2.78$, 1 d.f., $P = 0.10$). The juvenile sex ratio (male:female) in the future treated zone was 1.63:1, and that observed in the future untreated zone was 0.82:1 ($X^2 = 2.59$, 1 d.f., $P = 0.11$). The pretreatment age classes by sex distributions for the zonal subpopulations were not statistically different ($X^2 = 4.00$, 5 d.f., $P = 0.54$), although the number of animals on the treatment site was substantially greater than on the untreated. Application of zinc phosphide in 1981 eliminated 98.7% of the marked prairie dogs in the treatment site and 100% in 1982.

The distribution of animals into categories by age class and sex (Table 2) showed the

TABLE 1. Age-class distribution by sex of pretreatment black-tailed prairie dog subpopulations.

Pretreatment populations (1981):

	Future treated zone			Future untreated zone		
Age class	Males	Females	Total	Males	Females	Total
Adults	9	11	20	4	8	12
Yearlings	3	3	6	1	2	3
Juveniles	31	19	50	18	22	40
	43	33	76	23	32	55

TABLE 2. Age-class distribution by sex of posttreatment black-tailed prairie dog subpopulations.

Posttreatment populations (June–August 1982 and 1983):

	Immigrants			Residents		
Age class	Males	Females	Total	Males	Females	Total
1982:						
Adults	5	2	7	6	11	17
Yearlings	8	11	19	3	4	7
Juveniles	0	0	0	20	15	35
	13	13	26	29	30	59
1983:						
Adults	3	2	5	5	13	18
Yearlings	8	6	14	3	5	8
Juveniles	0	0	0	22	20	42
	11	8	19	30	38	68

resultant population was not homogeneous during either posttreatment year (1982: $X^2 = 40.09$, 5 d.f., $P < 0.01$; 1983: $X^2 = 37.10$, 5 d.f., $P < 0.01$). There were more yearling females and yearling males than expected on treated sites. Garrett and Franklin (1982) reported a high percentage of yearling males (91%) in the male intercolony immigrant population in Wind Cave National Park, South Dakota. However, their study of intercolony dispersal showed that 57% of the female prairie dogs captured were adults (Garrett and Franklin identified two-year-olds, and > two-year-olds), which differed strongly from our findings; only 15% were adults during 1982, 25% during 1983. It should be noted that, while Garrett and Franklin studied only long-distance intercolony dispersal of black-tailed prairie dogs, both intracolony immigration and short-distance intercolony dispersal were possible from two nearby colonies (Robert's and Hocking's dog towns). Of 64 immigrants captured in two years, only 5 previously marked immigrants (3 males, 2 females) were caught; 4 came from the adjacent untreated site (2 males, 2 females), and 1 male arrived from Hocking's dog town, less than 1 km from the edge of the study colony.

There was no observed reproductive success during either 1982 or 1983 among the newly established populations of prairie dogs on the treated site. This suggests that female black-tailed prairie dogs disperse after the mating season and do not bear young during their first year in a newly established territory. If this observation can be generalized to other populations, reports of females with juveniles directly following a control effort clearly indicate a failure to eliminate animals rather than the immigration of other prairie dogs.

Nonlactating females accounted for a greater proportion of the immigrant female subpopulation than expected (1982: $X^2 = 18.16$, 1 d.f., $P < 0.01$; 1983: $X^2 = 12.86$, 1 d.f., $P < 0.01$). Nonlactating females made up 100% (13/13) of the female immigrants in 1982 and 75% (6/8) in 1983. Nonlactating females on the control site made up only 11% (1/9) of the potentially reproductive population in 1982 and were not observed (0/12) in 1983. Because the majority of black-tailed prairie dogs in South Dakota are known to disperse between May and the early part of July (Garrett and Franklin 1982), well after their breeding season, dispersal in these individuals may

TABLE 3. Demographic ratios of prairie dogs during repeated trials on a colony where one side of the colony was treated with rodenticide (2% zinc phosphide) and a similar-sized zone was untreated. Prairie dogs in treated zones were first-year immigrants in both trials. Ratios were considered different at the $P < 0.05$ (2×2 contingency table, X^2, 1 d.f.).

	1982			1983		
Demographic ratios (x:1)	Immigrant	Resident	P	Immigrant	Resident	P
Population sex ratio	1.00	0.97	0.94	1.38	0.79	0.29
Adult sex ratio	2.50	0.55	0.11[A]	1.50	0.38	0.18[A]
Yearling sex ratio	0.73	0.75	0.97	1.33	0.60	0.38
Juvenile sex ratio	[B]	1.33	[B]	[B]	1.10	[B]
Adult males: yearling males	0.63	2.00	0.19[A]	0.38	1.70	0.12[A]
Adult females: yearling females	0.18	2.75	<0.01	0.33	2.60	0.02

[A] Non-significant P-value may be result of small sample size.

[B] No juveniles captured in treated site.

have been stimulated by their failure to reproduce. King (1955) reported that females immigrated after weaning juveniles, leaving territories to their young. This may be the case for some females, especially older individuals that are among populations of dispersers. However, Hoogland (1985) has demonstrated that the success of reproductive efforts of female prairie dogs may ultimately hinge upon defending nestling offspring from infanticidal females within the territory.

Two yearling females, captured within 25 m of each other as juveniles during August 1981 within the untreated zone, were recaptured as immigrants to the treated zone in June 1982. Both traveled over 400 m to their newly acquired territories. Both females showed no signs of having lactated during that season. By August 1982 one female had returned to her untreated natal territory. A similar instance of a returning immigrant was observed by Garrett (1982). In our study this same female again immigrated into the treated area in 1983. At the time of her second immigration, she showed signs of previous lactation.

Immigrants formed a transient subpopulation. In 1982 only 54% (14/26) of the immigrants were captured during both trapping sessions, compared to 73% (43/59) of the residents ($X^2 = 2.96$, 1 d.f., $P = 0.09$). Again in 1983 fewer immigrants, 47% (9/19), were captured in both sessions than were untreated animals, 68% (46/68), though the immigrant distribution was not significantly different from the expected ($X^2 = 2.63$, 1 d.f., $P = 0.11$). King (1955) also reported that during colony expansion newly established territories were occupied by highly unstable populations where many different adults were trapped over a short period of time.

The study adds to the evidence that marked demographic differences exist between resident, undisturbed black-tailed prairie dog populations and those of immigrants. We observed that nonreproductive females comprised a large proportion of the female immigrants each year. During our study female immigrants did not produce young in their new territories during the year in which they dispersed. Also, immigrants who seem to have settled into burrows are likely to "disappear" at a greater rate than expected. Clearly, the complexity in the nature of prairie dog dispersal is just one more factor that indicates the need for careful, intensive management of colonies in parks, refuges, and on grazed public land.

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WESTERN PAINTED TURTLE IN GRANT COUNTY, OREGON

Jeffrey H. Black[1] and Andrew H. Black[2]

ABSTRACT.—The western painted turtle, *Chrysemys picta belli* (Gray), is recorded for the first time from Grant County, Oregon. This specimen represents the southwesternmost occurrence of the species in Oregon.

On 27 August 1984 a western painted turtle, *Chrysemys picta belli* (Gray), was collected in a small pond near Canyon City, Grant County, Oregon. This specimen represents the first record of this turtle in Grant County and the southwesternmost occurrence of this species in the state (Nussbaum, Brodie, and Storm 1983).

The turtle was observed swimming quietly on the surface of a one-acre pond filled with aquatic vegetation. The pond was on a sagebrush- and juniper-covered hillside adjacent to Canyon Creek on the west side of Canyon City. The pond is 1 km west of Canyon Creek and 6 km from the John Day River and mouth of Canyon Creek. Later the turtle was captured, sexed, measured, photographed, and released back into the pond.

The turtle was an adult female with a carapace length of 172.3 mm and width of 132.3 mm. Its plastron length was 164.5 mm and width 89.2 mm. She was heavy and appeared healthy. Nussbaum, Brodie, and Storm (1983) report females range from 95 to 210 mm in carapace length in the Willamette Valley of western Oregon.

Black and Storm (1970) reported a northwestern pond turtle, *Clemmys marmorata marmorata* (Baird and Girard), from Grant County and noted the sightings of other turtles in ponds bordering the John Day River in Grant County. Northwestern pond turtles and western painted turtles have probably moved from the Columbia River southwestward in the John Day River to Grant County. There are records of western painted turtles in Umatilla, Morrow, and Union counties, all north of Grant County but south of the Columbia River in eastern Oregon. The possibility also exists that the turtle was captured elsewhere or purchased as a pet and then released into the pond or area where it was captured.

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AMERICAN SWALLOW BUG, *OECIACUS VICARIUS* HORVATH (HEMIPTERA: CIMICIDAE), IN *HIRUNDO RUSTICA* AND *PETROCHELIDON PYRRHONOTA* NESTS IN WEST CENTRAL COLORADO

Thomas Orr[1] and Gary McCallister[1]

ABSTRACT.—*Oeciacus vicarius* bed bugs were collected from 32% of *Hirundo rustica* nests and 83% of *Petrochelidon pyrrhonota* nests on bridges in western Colorado in December 1984. A total of 409 bugs (158 adults and 251 juveniles) were counted in 47 nests, two months after the hosts had departed for the winter.

Two regular avian visitors to the Colorado River system in west central Colorado are the cliff swallow, *Petrochelidon pyrrhonota*, and the barn swallow, *Hirundo rustica*. They spend the warm late spring to autumn months in North America and winter in South America (Knopf 1977). The cliff swallow builds a gourd-shaped mud nest lined with grass and feathers beneath bridges and on natural cliff faces. The barn swallow builds an open nest with mud pellets and lined with feathers and straw under bridges or on buildings.

Oeciacus vicarius Horvath, the American swallow bug, has been previously reported from *Petrochelidon* (Meyers 1928) at Dolores, Colorado (Gillette and Baker 1895). Usinger (1966) lists *Hirundo* as a rare host, but some controversy seems to exist over host specificity. The previous report of *O. vicarius* in Colorado was from the inhabited nests in the spring of the year.

In this paper we report on the incidence of *O. vicarius* in both barn swallow and cliff swallow nests during December in west central Colorado, a new geographic area.

MATERIALS AND METHODS

In December 1984, 41 barn swallow nests and 6 cliff swallow nests were collected from beneath highway bridges west of Fruita, Colorado. They were placed into plastic bags, numbered, and sealed. Six nests at a time were weighed and then processed under Berlese funnels for six to eight hours. Visual examination and additional manual extraction of the bugs followed. Specimens were collected into 70% ethanol. Mites, ticks, spiders, moths, and dermestids were included, but the most abundant species was *Oeciacus vicarius*.

These were identified under magnification (10X to 400X) using Slater and Baranowski's (1978) key to the true bugs. The immature stages were identified (I, II, III, IV, V) with a key in Usinger (1966). Some specimens were mounted using standard techniques in balsam on glass slides; others were mounted and cleared in lactophenol for photographs.

A total of 409 *Oeciacus vicarius* specimens was collected. Of 158 adults, 99 were male, 59 female. There were 39 stage I, 44 stage II, 49 stage III, 85 stage IV, and 24 stage V instars, a total of 251 immatures. Table 1 shows the composition of the population in each kind of nest.

Two hundred forty-eight bugs were in 13 of the 41 barn swallow nests, a prevalence of 32%. This is a mean of 19 bugs per infested nest; numbers ranged from 1 to 68 per nest. One hundred sixty-one bugs were in 5 of the 6 cliff swallow nests (prevalence = 83%), a mean of 32 bugs per infested nest, with numbers ranging from 2 to 103 per nest. It should be noted that the *P. pyrrhonota* nests are much bulkier ($\bar{x}$ = 451 g/nest) than the *H. rustica* nests ($\bar{x}$ = 199 g/nest). This means that there was 1 bug per an average of 96 gm of *Hirundo* nest and 1 bug per 70 gm of *Petrochelidon* nest.

DISCUSSION

The doubling of the spermalege in *Oeciacus*

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TABLE 1. *Oeciacus vicarius* population in *H. rustica* and *P. pyrrhonota* nests in December 1984.

Host nest	Adults			Instar stages					
	M	F	Total	I	II	III	IV	V	Total
H. rustica	67	46	113	27	16	27	50	15	135
P. pyrrhonota	32	13	45	12	28	32	35	9	116

vicarius was noted by Cragg (1920) and Abraham (1934). Ludwig and Zwanzig (1937) reported it in 0.5 to 40% of the females in the populations they studied. In the present case it occurred in 1.7% of the females.

The red body color seen in some stage V instar nymphs is not mentioned in the literature, although Spencer (1930) describes a white specimen. This anomaly of red body occurred in 4.2% of the stage V instars.

Meyers (1928) names *Petrochelidon lunifrons* as a host but dismisses *Hirundo erythrogaster*. Usinger (1966) lists *P. albifrons* and, more rarely, *H. erythrogaster*. This study demonstrates this parasite in the winter nests of two additional hosts: *P. pyrrhonota* and *H. rustica*. It tends to support the claim that the barn swallow may be a less common host. It also establishes the geographic distribution of the parasite in a previously unreported area.

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PSEUDOCROSSIDIUM AUREUM (BARTR.) ZAND. (POTTIACEAE, MUSCI) NEW TO UTAH

John R. Spence[1]

ABSTRACT.—*Pseudocrossidium aureum* (Bartr.) Zand. (Pottiaceae, Musci) is reported as new to Utah from a locality in Wayne County. The species distribution is noted and comparisons are made with the other three species of *Pseudocrossidium* found in North America.

Despite excellent recent floras for Utah (Flowers 1961, 1973), the bryophyte flora of the state remains incompletely known. This is even more obvious for the intermountain region (sensu Cronquist et al. 1972). Recent studies that have concentrated on dryland bryophyte floras (e.g., Magill 1976, Stark and Castetter 1982, McIntosh 1986) emphasize the diversity of dryland bryophytes. The studies of Magill and McIntosh in particular, which concentrated on intensive collecting in small regions, indicate that many elusive and poorly known bryophytes remain to be discovered in the western drylands.

While conducting studies on the bryophyte flora of southern Utah, I collected a species of *Didymodon*, which proved upon identification to be *D. vinealis* (Brid.) Zand. Intermixed with the *Didymodon* were a few small sterile plants that keyed to *Pseudocrossidium aureum* (Bartr.) Zand. using the key in Zander (1979). A duplicate of the collection was confirmed by Dr. Zander of the Buffalo Museum of Science. This species was not previously known from Utah, and the nearest known populations are in southern Coconino County in Arizona (Haring 1961). The site information and associated species for this collection were:

Utah: Wayne Co., Capitol Reef National Park, near the Rim Overlook. Growing intermixed with *Didymodon vinealis* at base of cliff of Navajo Sandstone in shaded, north-facing alcove on dry sand. In slickrock and pinyon-juniper communities, with *Pinus edulis, Juniperus osteosperma, Shepherdia canadensis, Coleogyne ramosissima, Bouteloua gracilis, Yucca* ssp., and *Opuntia* ssp. Elevation 2,195 m, 26 November 1986, Spence 3319a. pH of sand = 6.0 (pHydrion paper). Deposited in BUF and my personal herbarium.

Pseudocrossidium aureum was originally described from the Santa Catalina Mountains of southern Arizona as *Tortula aurea* (Bartram 1924). The transfer to *Pseudocrossidium* was made by Zander (1979). An important component of the bryophyte stratum in the Sonoran and Chihuahuan deserts (Magill 1976, Nash et al. 1977), its distribution is Texas, Oklahoma, New Mexico, Arizona, Utah, California, and northern Mexico. Apparently it has not yet been reported from the Mohave Desert of California, Nevada, and Utah (Harthill et al. 1979). The Utah locality is several hundred miles north of the nearest previously reported locality in Arizona. It also occurs at a relatively high elevation compared to the rest of its distribution.

The genus *Pseudocrossidium* is distinguished from the related genera *Barbula, Tortula*, and *Bryoerythrophyllum* by *inter alia* its differentiated perichaetial leaves, strongly revolute leaf margins, and lack of an adaxial stereid band in the costa (Zander 1979, 1981). *Pseudocrossidium aureum* lacks many of the features of the genus, and sporophytes remain unknown (Zander 1981). The species has been illustrated by Bartram (1924), Steere (1938), Crum and Anderson (1981), and Zander (1981).

Three additional species of *Pseudocrossidium* are known from western North America. These are *P. hornschuchianum* (Schultz) Zand., *P. replicatum* (Tayl.) Zand., and *P. revolutum* (Brid. in Schrad.) Zand. *Pseudocrossidium aureum* is distinguished from these species by its conspicuous, yellowish-reddish, smooth awn. The other three species are generally apiculate or mucronate. The Eurasian species *P. hornschuchianum* has been reported from a botanic garden in Vancouver, British Columbia, and may be introduced (Tan et al. 1981). Another Eurasian species, *P. revolutum*, also occurs in California, Oregon, Washington, Idaho, British Columbia, Yukon Territory, and the Canadian Arctic Archipelago. The species *P. revolutum* is an important component of the shrub-steppe of Oregon, Washington, and British Columbia (McIntosh 1986). *Pseudocrossidium replicatum* has a distribution similar to *P. aureum*, although it is also found in the Andes of South America. Its North American distribution is Texas, New Mexico, Arizona, and Mexico (Zander 1979).

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RELATIONSHIP OF WESTERN JUNIPER STEM CONDUCTING TISSUE AND BASAL CIRCUMFERENCE TO LEAF AREA AND BIOMASS[1]

Richard F. Miller[2], Lee E. Eddleman[3], and Raymond F. Angell[2]

Abstract.—The ability to measure leaf area and biomass on a plant community basis has many important ecological applications. These include quantification of gas exchange, use of water resources on the site, nutrient pools, and construction of models simulating production and resource allocation. To test a nondestructive technique for estimating leaf area and leaf biomass of western juniper (*Juniperus occidentalis* Hook.), sapwood area and basal circumference were evaluated as predictors of total leaf biomass and leaf area. Nineteen trees, ranging in size from 9.0 to 263 cm in circumference, were destructively sampled. The entire leaf biomass was harvested and measured, and regression equations were developed. Both sapwood area and basal circumference significantly ($P < .01$) correlated with projected leaf area and leaf biomass (r values = 0.98).

Knowledge of leaf area and leaf biomass on a plant community basis has many important ecological applications. Leaf area is important in gas exchange, the hydrologic cycle, and models simulating production and resource allocation. Leaf area is essential in assessing recovery rates in forested ecosystems following disturbance (Sollins et al. 1974). Waring et al. (1980) also found leaf area in combination with the annual growth increment of a tree (annual growth increment cm^2:leaf area m^2) a useful index for assessing vigor in conifers. Defining leaf biomass for a dominant species describes the size of a major nutrient and carbon pool in a plant community.

Measuring leaf area, on a whole plant basis, is difficult because of a high degree of variability among plants and across sites. Leaf area measurements are also labor intensive and often require destructive sampling. As a result of these difficulties, little information is available on leaf area in range ecosystems. Foresters have successfully used sapwood area to indirectly estimate leaf area. Shinozaki et al. (1964) concluded that a constant cross-sectional area of conducting tissue supports a given unit of leaves. Since that time, researchers have found close relationships between sapwood area and leaf area (Dixon 1971, Grier and Waring 1974, Waring et al. 1977, Snell and Brown 1978, Whitehead 1978, Kaufmann and Troendle 1981, Marchand 1984). The correlation between leaf area and area of conducting tissue is presumably a function of the physiological balance between water demand by the crown and the ability of the stem to conduct water (Kaufmann and Troendle 1981). Application of this hypothesis, sometimes called the pipe model theory, is discussed by Waring et al. (1982).

Estimating the impact of western juniper (*Juniperus occidentalis* Hook.) woodlands on nutrient resources and the hydrologic cycle requires estimates of leaf area and biomass. The objective of this study was to develop a useful, nondestructive technique for estimating leaf area and leaf biomass of western juniper woodlands by testing the pipe model theory. To do so, we evaluated the relationship between sapwood area and basal circumference with leaf biomass and leaf area.

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MATERIALS AND METHODS

The study site is at the Squaw Butte Experimental Range on the northern fringe of the Great Basin in southeastern Oregon, 57 km west of Burns. The 40-year mean precipitation for this area is 300 mm. The study site is a mountain big sagebrush/Idaho fescue (*Artemisia tridentata* ssp. *vaseyana*/*Festuca idahoensis*) habitat type (Winward 1970) at an elevation of 1,350 m. Soils are fine-loamy, mixed, frigid Aridic Durixerolls, approximately 112 cm deep to columnar basalt.

Thirteen healthy trees ranging from 9 to 263 cm in circumference (2.9–84 cm in diameter) at the litter surface were selected for destructive sampling. Trees selected had full canopies showing no signs of insect damage or disease. Trees were subjectively selected so four trees would fall within each of three size classes: 2.5–6 cm, 6–20 cm, and 20–45 cm in basal diameter. The thirteenth tree was selected to represent the largest trees within the stand. All trees were single stemmed. Sampling was conducted from 20 June to 1 October 1984. Maximum error caused by the duration of sampling during the growing season is estimated to be 15% (Miller and Shultz 1987). Trees were divided into two segments along the main trunk (base and midsection). Sapwood area was measured at both points, and all foliage on branches attached to the main trunk above the point of sapwood measurement and basal circumference was removed, dried at 60 C for 72 hours, and weighed. Sapwood area and basal circumference were measured at the litter surface because of tree growth form. Sapwood was easy to distinguish from heartwood, particularly after several days of air drying. A piece of acetate was laid over the stem base and the sapwood area was outlined. A cut-out of the outlined sapwood was constructed from black paper and the area of the paper measured on a leaf-area meter. All or most of the limbs were removed prior to felling the tree. One sample of approximately 0.1 kg of fresh leaf material was harvested from each tree during defoliation, sealed in plastic bags, and stored in a freezer for later evaluation of leaf weight to leaf area relationships.

Frozen samples of foliage were thawed in the lab and their areas measured on a Li-Cor leaf-area meter. Foliage was assumed to be cylindrical, so leaf-area readings were multiplied by π to compute total exposed leaf surface. Due to partial overlapping of lower adjacent leaves, total leaf surface area is underestimated (we estimated approximately 10%). Estimates of total gas exchange, however, will not be over- or underestimated as long as measurements per unit leaf area are also based on exposed leaf area. Following leaf-area measurements, samples were dried at 60 C for 72 hours, weighed, and added to the total foliage weight for the tree. Linear regression procedures were used to establish a relationship between leaf biomass (dry weight) and leaf area for both populations of trees. These equations were then used to convert total harvested leaf biomass to total leaf area for each tree.

In the following year a second population ($n = 6$) of trees at two sites in central Oregon, 175 km west of Squaw Butte, was selected for study. The relationship between sapwood area and basal circumference with leaf area in the second population was compared to the first. Habitat types at both locations were similar to the site sampled at Squaw Butte. Trees, ranging in circumference from 11 to 47 cm, were sampled similarly to those in the previous year.

Values representing the ratios of leaf area (m^2) to sapwood area (cm^2) and leaf area (cm^2) to leaf weight (g) were derived for each of the trees sampled. Student's t-test was used to test the null hypothesis that mean ratios were identical between the two populations of trees sampled. The null hypothesis was accepted and data for the two populations were pooled for final analysis.

Basal circumference, basal sapwood area, and midsection sapwood area served as independent variables in regression analysis aimed at predicting total leaf area or total leaf biomass of the supported foliage. Possible differences in relationships derived from basal sapwood areas and midsection sapwood areas

TABLE 1. Regression equations, standard error of estimate (Sy.x), and correlation coefficents for estimating leaf biomass and leaf area.

n	Independent variable (X)	Dependent variable (Y)	Regression equation	Sy.x	Correlation coefficient
19	Leaf wt (g)	Leaf area (cm^2)	$Y = -40.566 + 65.238X$	107.010	0.978
19	Sapwood area (cm^2)	Leaf biomass (kg)	$Y = 1.237 + 0.024(X) + 0.00005(X^2)$	2.735	0.987
19	Sapwood area (cm^2)	Leaf area (m^2)	$Y = 8.145 + 0.155(X) + 0.00035\,(X^2)$	17.822	0.987
19	Basal circ. (cm)	Leaf biomass (kg)	$Y = -5.381 + 0.352(X)$	3.570	0.976
19	Basal circ. (cm)	Leaf area (m^2)	$Y = -35.036 + 2.296(X)$	23.294	0.976
13[1]	Sapwood area (cm^2)	Leaf biomass (kg)	$Y = 0.473 + 0.040\,(X)$	0.445	0.938
13	Sapwood area (cm^2)	Leaf area (m^2)	$Y = 0.220 + 0.504(X) - 0.0024\,(X^2)$	3.250	0.906
13	Basal circ. (cm)	Leaf biomass (kg)	$Y = -1.046 + 0.143\,(X)$	0.391	0.953
13	Basal circ. (cm)	Leaf area (m^2)	$Y = -4.007 + 0.767(X)$	3.763	0.862

[1] Regression equations with n = 13 were developed for trees with basal circumferences less than 50 cm.

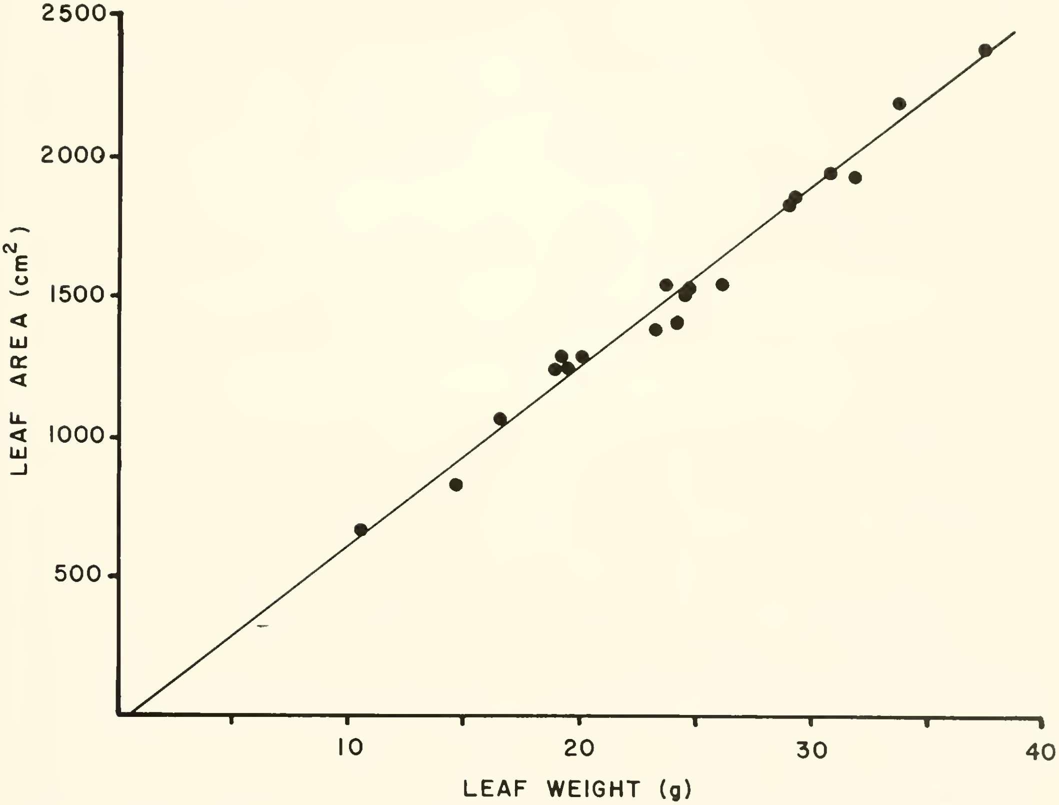

Fig. 1. Regression line and data points for leaf dry weight and leaf area for western juniper with n = 19, Sy.x = 107.010, and r = 0.978.

were evaluated by comparison of regression lines (Neter and Wasserman 1974). Regression lines were also compared between all trees sampled (n = 19) and with the big tree (263 cm in circumference) excluded. Appropriateness of the models finally selected to predict total leaf area or biomass was evaluated by ordering data in accordance with the independent variable and examining the residuals. Rank correlation of residuals with independent variables (Neter and Wasserman 1974) failed to reject the null hypothesis of constant variance ($P > .05$).

RESULTS

A strong linear relationship between leaf weight and surface area of leaves allowed us to

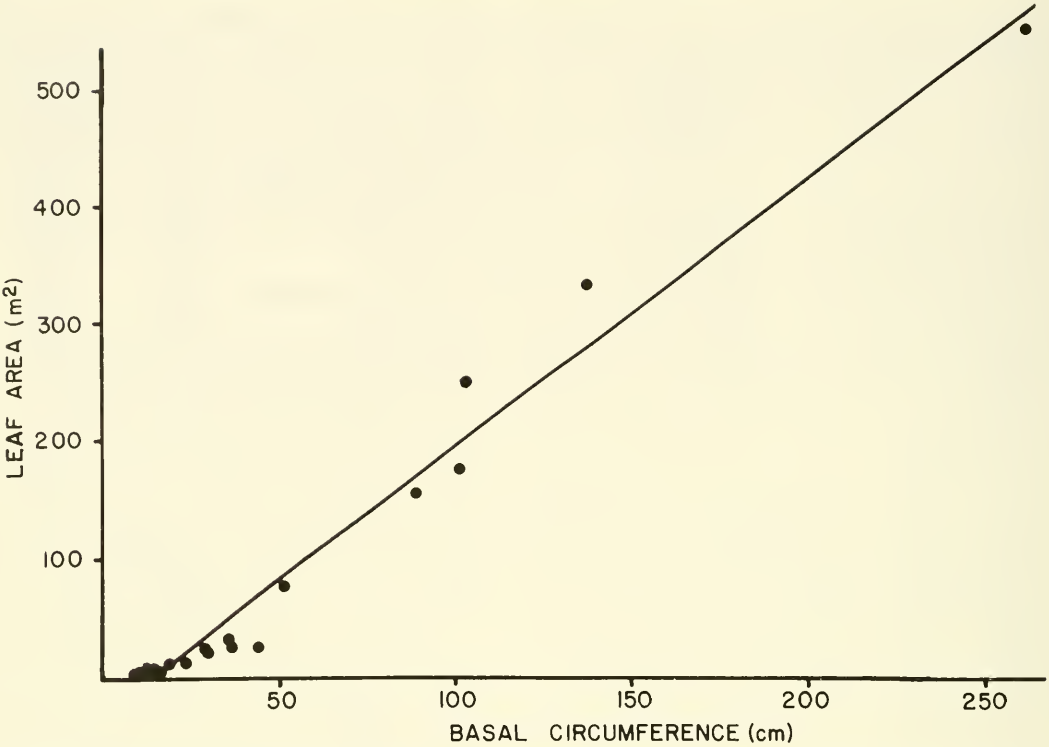

Fig. 2. Regression line and data points for basal circumference at the litter surface and total leaf area for western juniper with n = 19, Sy.x = 23.294, and r = 0.976.

estimate leaf area by measuring leaf weight (Table 1, Fig. 1). Sapwood area and basal circumference were significantly ($P < .01$) correlated with leaf area (Fig. 2). Estimates, however, can be improved for small trees (primarily for trees with basal diameters < 20 cm) if the regression equation developed for trees less than 50 cm in circumference is used. The large tree did not significantly ($P \geq .10$) change the slope or intercept of the regression line when included with the 18 smaller trees (Neter and Wasserman 1974).

Relationships between leaf area and sapwood area measured at the tree base, and leaf area and sapwood area midway up the trunk were significantly different ($P < .05$). At the tree base 1 cm^2 of sapwood supported 0.45 m^2 of leaf area. At the tree's midsection 1 cm^2 of sapwood supported 0.64 m^2 of leaf area. Gholz (1980) reported a leaf-area:sapwood ratio of 0.56 for western juniper when sapwood was measured at DBH.

DISCUSSION

Results of this study support use of the pipe model theory on western juniper. Both sapwood area and basal circumference are useful measurements for estimating total leaf area or leaf biomass. Caution should be used when extrapolating equations to trees larger than the largest tree (diameter = 82.8 cm, height = 9.8 m) measured in this project, since the last data point strongly influences the shape of the curve. Few trees, however, in a mature stand of western juniper will be substantially larger. The leaf-area model using basal circumference may also perform poorly on decadent stands of western juniper. Because young trees usually constitute only a small proportion of total leaf area or biomass in mixed-aged stands of juniper, the fact that the curve does not pass through the origin will add little error to an overall estimate of total leaf area for a western juniper woodland. If the stand is young, however, with numerous basal circumferences less than 50 cm, the regression model developed for small trees will improve the estimates.

The strong correlation between basal circumference and total leaf area is probably due to the significant ($P < .01$) relationship between sapwood area and basal circumference

($r = 0.98$). Ovington et al. (1968) found a high correlation between bole cross-sectional area and leaf area in young *Pinus radiata*. Cross-sectional area, however, closely correlated with sapwood area since young trees have little or no heartwood.

The relationship between sapwood area and leaf area in western juniper changes above the litter surface. Less sapwood area is required to support a unit of leaf area as one moves up the trunk. This relationship, supported by both our work and that of Gholz (1980), may be partially due to butt swell. Waring et al. (1982) also reported a reduction in sapwood area along the trunk of *Pseudotsuga menziesii* below the live crown. In *Chamaecyparis obtusa*, Morikawa (1974) concluded that linear correlations should not extend much below breast height, particularly below butt swell. Because of western juniper's growth form, however, sapwood area should be measured at the base. If multiple stems are present, each stem circumference should be measured separately.

Ratio of leaf area to sapwood cross-sectional area (leaf area m^2:sapwood area cm^2) reported for 14 other conifer species ranged from 0.16 to 0.75 (Waring et al. 1982). In general, larger coefficients are found in tree species growing in more mesic environments, while trees with smaller coefficients are typical of drier environments (Kaufmann and Troendle 1981, Waring et al. 1982). When compared with other conifer species, the ratio between total leaf area to sapwood area in western juniper (0.45) is higher than might be expected for a tree growing in a relatively dry environment. Western juniper, however, has relatively low stomatal conductance rates per unit leaf area compared with other conifers and contains leaf morphological characteristics which avoid drought and reduce moisture loss (Miller and Shultz 1987). Factors reducing water loss through transpiration from the crown would reduce the amount of sapwood tissue required to support a unit of leaf area.

Gholz (1980) used basal circumference measurements to estimate leaf biomass and leaf area for western juniper. His study plots are within 1 km of our study plots, located 175 km west of Squaw Butte. His model (ln leaf biomass $= -4.243 + 1.5606 \ln$ [basal circumference]) fit our data closely for trees < 30 cm in circumference, but consistently underestimated leaf biomass for trees 30 to 137 cm in circumference by 24 to 47%. Differences may be attributed to sampling procedures. Gholz subsampled trees ($n = 10$) instead of sampling entire trees. We suspect the difficulty of accurate subsampling would increase with an increase in tree size. Another source of difference between the two studies was the relationship between leaf weight and leaf surface area. Our ratios (cm^2:g) at both sites were larger than Gholz's.

The relationship between sapwood area and leaf area in western juniper did not change between locations. We hypothesize that geographic range and environmental conditions between these two study sites were not large enough to cause differences in leaf-area:sapwood-area coefficients. Marchand (1984) reported no change in leaf-area: sapwood-area coefficients for *Abies balsamea* and *Picea rubens* growing across an environmental gradient. Variation, however, in the relationship between sapwood area and leaf area has been reported within species with large geographical distributions (Waring et al. 1982). An example is *Pseudotsuga menziesii* with a leaf-area: sapwood-area (m^2/cm^2) coefficient of 0.54 for Pacific Coastal trees (Waring et al. 1982) and 0.34 for trees growing in the Rocky Mountains (Snell and Brown 1978).

Total leaf surface area or biomass for a western juniper woodland can be estimated by multiplying the mean basal circumference or sapwood area of trees in the stand (obtained through subsampling the stand) by tree density (obtained from subsampling or aerial photos). Estimates of basal circumference or sapwood area of a western juniper woodland should provide good estimates of total leaf area or leaf biomass. Estimates based on sapwood areas will probably be more reliable, especially in decadent stands of juniper, than estimates made from basal circumference. Models based on circumference, however, provide us with a nondestructive and less labor-intensive means of estimating leaf areas. Development of models estimating leaf biomass or leaf area for various plant species will enhance our ability to determine their impact on the hydrologic cycle through transpiration and to identify total carbon fixation capabilities and nutrient pools.

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PARASITES OF THE BOWHEAD WHALE, *BALAENA MYSTICETUS*

Richard A. Heckmann[1], Lauritz A. Jensen[2], Robert G. Warnock[3],
and Bruce Coleman[1]

ABSTRACT.—Blood, tissue, and organ samples from five bowhead whales were examined for ecto- and endoparasites. Two species of protozoans, four genera of diatoms, one species of trematoda, two species of nematoda, and one species of amphipoda "louse" were found. No blood parasites were recovered. The larval anisakid nematode, found in the submucosa of the forestomach of one whale, generated a prominent inflammatory response. Protozoans found in contents of the colon included a flagellate and a sarcodinan. The sarcodinan, which was common in the colon contents of one whale, belongs to the genus *Entamoeba* and probably represents an undescribed species. *Ogomogaster plicatus*, a trematode, was also identified. The data from this study are compared with previous lists of parasites for the bowhead whale and two other species of baleen whales. From the results presented, the previous list of parasites for the bowhead whale has been expanded to include eight additional genera and species.

Cetaceans throughout the world are known to be infested and infected with parasites (Dailey and Brownell 1972). This does not necessarily mean that the hosts are seriously affected or damaged by the symbionts. If, in addition to the parasite load, stress and/or nutritional imbalances occur, the animal may become weak and possibly die. Stroud and Roffe 1979, Dailey and Walker 1978, Martin et al. 1970, Ridgway and Dailey 1972 have indicated that helminths were a possible factor for cetacean strandings. Stranded animals exhibited disoriented behavior with an obvious loss of equilibrium. Necropsy results of these animals showed that the central nervous system was infected with trematodes of the genus *Nasitrema*, thus providing at least a partial explanation for the whale strandings. The nematode *Sternurus*, located in the ears of cetaceans, is also a potential factor for cetacean strandings. The brains of these stranded animals showed lesions induced by trematode eggs.

Activities associated with offshore oil and gas development, such as those in the Beaufort Sea, may increase the stress to bowhead whales and thereby allow an increase in parasite burden. It would be advantageous to determine the types of parasites harbored by bowhead whales for such knowledge would help in understanding what effect contact with spilled oil may have on cetaceans.

The primary objective of this study was to estimate the parasite burden of the bowhead whale, *Balaena mysticetus*, through the examination of the selected specimen materials obtained from subsistence harvested whales.

METHODS

Specimen materials were obtained from five bowhead whales taken off Barrow, Alaska, in 1980 by Eskimo hunters. Tissue samples, including colon contents, were collected onsite (Albert 1981), fixed in 10% formalin, and shipped by air freight to the parasitology laboratory at Brigham Young University. Blood smears from whales were air dried and sent with the above samples. The samples were processed as follows:

TISSUES AND ORGANS.—After the code number for the whale was recorded, each specimen was weighed, measured, and then dissected to determine the presence of parasites. Intestinal segments were cut lengthwise, after which the lumen was examined for macroscopic parasites. Samples of lumen contents were placed on glass slides and examined with a light microscope. Slides of lumen contents from the intestine were also fixed and stained with iron haemotoxylin, trichrome, or Giemsa-Wrights stains to enhance parasite presence. After the staining procedure was completed, each slide was examined for para-

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TABLE 1. Bowhead whale, *Balaena mysticetus*, specimens examined for parasites.

Whale number (Code)	Type of specimen	Specimen length (cm)	Specimen weight (kg)
80B1	Blood smears (4 slides)	—	—
	Intestine segments:		
	A	83	7.3
	B	107	8.6
	C	99	3.15
	D	134	2.25
80B2	Blood smears (2 slides)	—	—
	Intestine segments:		
	A	87	6.75
	B	59	3.15
	Liver sample	—	2.7
80B7	Blood smears (2 slides)	—	—
	Intestine segments:		
	A	78	1.21
	B	75	2.41
	C	44.5	4.70
	Liver sample	—	2.3
	Diaphragm sample	—	0.7
	Colon contents (1.5 liters)	—	—
80B8	Blood smears (2 slides)	—	—
	Intestine segment	96	4.5
	Diaphragm sample	—	0.6
80B9	Louse on baleen	—	—
	Liver sample	—	1.35
	Colon segment	95	9.9

sites. Pieces of liver and diaphragm were placed in separate jars containing a standard digestive enzyme solution (pepsin and hydrochloric acid in water) for 24–48 hours at 37 C. This procedure digests host tissue but not nematode larvae and adults. The material was then centrifuged and examined with a light microscope.

COLON CONTENTS.—Formalin-fixed colon contents were examined following the same procedure as outlined for lumen contents from the intestine. The same stains were used for the preparation of permanent slides.

BLOOD SMEARS.—Standard methods were followed for the examination of blood smears for parasites. A combination Giemsa-Wrights stain was used for maximum staining of any intracellular and extracellular parasites that might be present. Each stained slide was examined for at least 10 minutes at 400X and 1,000X magnification.

PARASITE PROCEDURE.—Two procedures were used for flukes. Fluke specimens were fixed in alcohol-formalin-acetic acid (AFA) and gluteraldehyde. Those fixed in AFA were stained with semichon's carmine and mounted on glass slides. Gluteraldehyde fixative in an acrolien buffer was used for flukes to be examined with scanning electron microscopy (SEM). For SEM each fluke was critically point dried, mounted on a specimen holder, coated with gold for three minutes with a CS mini-coater sputter, and then viewed with an AMRAY 1000A scanning electron microscope operating at 20 Kv. A whale louse, *Cyamus ceti*, was also examined with SEM.

A paraffin block of tissue containing a larval nematode (Migaki 1981) was prepared for histological evaluation, and sections were stained with haemotoxylin and eosin, trichrome and periodic acid-Schiff. An intact nematode found free in the stomach of a bowhead whale was also examined.

Skin samples representing normal and eroded areas were provided for parasite examination (Haldiman et al. 1981). These samples were prepared for SEM and light microscopy as explained for flukes and nematodes.

Results of the parasite examination were summarized and compared with the existing list for the bowhead whale, *B. mysticetus*,

TABLE 2. Results of examining bowhead whale, *Balaena mysticetus*, tissue samples, with process procedures summarized, for parasites.

Whale number	Tissue examined	Special procedures	Parasites observed
80B1	Bloood smears	Giesma-Wright stain	None
	Intestine segments:		
	A		None
	B		None
	C		None
	D		None
	Intestinal contents		Larval nematode
80B2	Blood smears	Giesma-Wright stain	None
	Intestine segments:		
	A		4 trematodes
	B		2 trematodes
	Liver sample		None
	*Liver sample	**Digestive fluid	None
80B7	Blood smears	Giesma-Wright stain	None
	Intestine segments:		
	A		None
	B		None
	C		8 trematodes
	Liver sample		None
	*Liver sample	**Digestive fluid	None
	Diaphragm sample		None
	*Diaphragm sample	**Digestive fluid	None
	Colon contents	Fixed in formalin stained with three stains	2 protozoan species Amoeboid form Flagellate form
80B8	Blood smears	Giesma-Wright stain	None
	Intestine segment		10 trematodes
	Diaphragm sample		None
	*Diaphragm sample	**Digestive fluid	None
80B9	Baleen piece		"Louse" attached (*Cyamus* sp.)
	Liver sample		None
	*Liver sample	**Digestive fluid	None
	Colon		None

*Small pieces were removed from the samples of liver and diaphragm and placed in breakers containing digestive fluid

**Digestive fluid. An aqueous solution of pepsin and hydrochloric acid used to digest host tissue and leave nematodes intact

gray whale, *Eschrichtus robustus*, and blue whale, *Balaenoptera musculus*.

RESULTS

Table 1 lists the specimens obtained for this study, with data on whale code number, type of tissue, and amount. The results of examining the pieces of tissue are listed in Table 2. Parasites obtained from these bowhead whale samples are indicated in the table, after which each parasite is listed separately and discussed.

Comments on Parasites Observed

Two species of protozoa, one amoeboid and one flagellated, were found in the formalin-fixed colon contents of one whale (80B7; Table 2). The amoeboid form appears to be a species new to science, while insufficient numbers of the flagellate negated further taxonomic study. Both represent the first known protozoa observed and described from bowhead whale intestinal contents.

Amoeboid Protozoan

Fig. 1

An unidentified amoeba from the colon contents of animal 80B7 had the following characteristics, based on the observation of 100 specimens in stained and fixed preparations: trophozoite and cyst stages, cysts containing one to four nuclei, cysts oval in shape ranging from 15 to 18 μm in diameter, nuclei

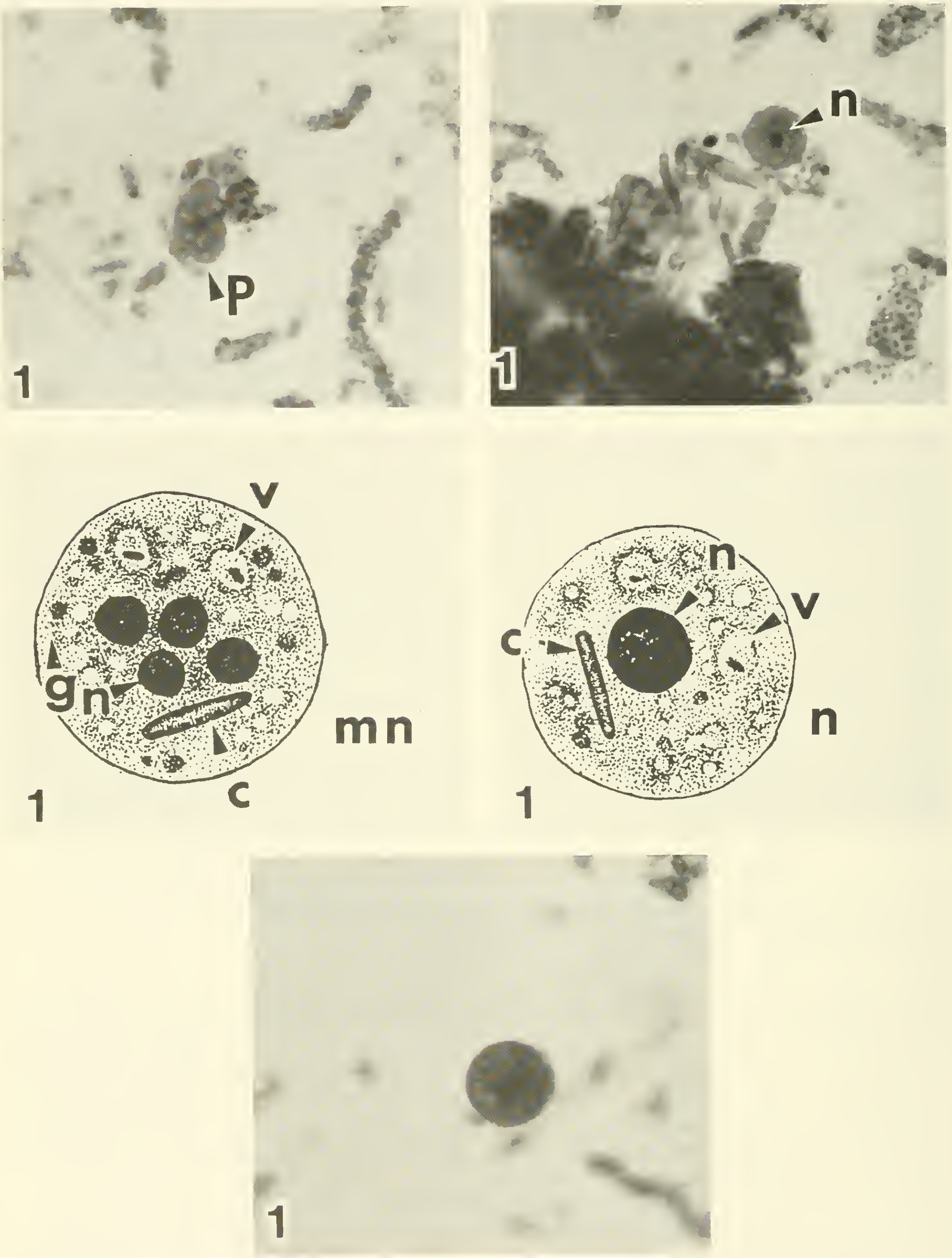


Fig. 1. Photomicrographs and line drawings of an amoeboid parasite (*Entamoeba* sp.) from the colon contents of a bowhead whale, *Balaena mysticetus*. Note the pseudopod (P) characteristic of this protozoan group, both single (n) and multinucleate (mn) cells, vacuoles (v), granular cytoplasm (g), and chromatoid body (c) (1,000X for photomicrographs).

spheroid to ovoid, nuclei randomly distributed for multinucleate forms and centrally located in uninucleate forms, nucleus occupies approximately 10% of the cell volume,

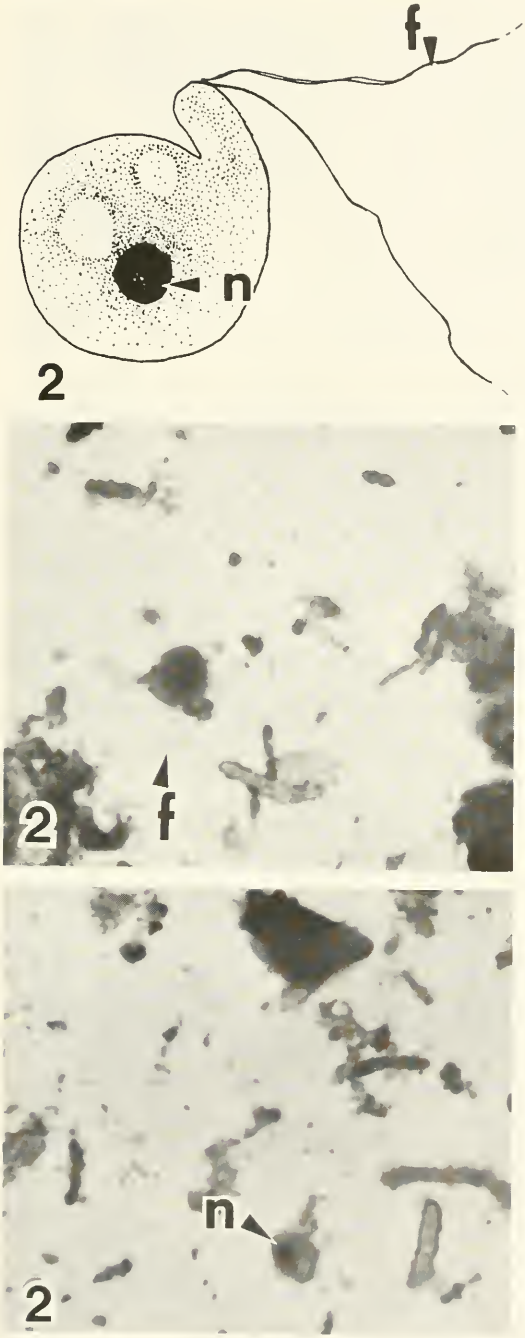


Fig. 2. Photomicrographs and line drawing of a flagellated protozoan found in the colon contents of *Balaena mysticetus*. Flagella (f) and a single nucleus (n) are visible, both characteristic of flagellated protozoa (1,000X for photomicrographs).

pseudopodia observed, vacuoles vary in number, both food and water vacuoles present chromatoidlike bodies in cytoplasm, peripheral nonchromatic granules, it was common in the intestinal contents of one bowhead whale. Based on these observations and the similarity of characteristics (Kudo 1966), we consider this amoeba a species of *Entamoeba* Casagrandi & Barbagallo, 1895. Thus, based on Levine et al. (1980), the classification for this amoeba would be:

Phylum:	Sarcomastigophora
Subphylum:	Sarcodina
Class:	Lobosea
Order:	Amoebida
Family:	Endamoebidae
Genus:	*Entamoeba* sp.

From further literature research and observations of this protozoan, the correct species will be determined. The genus *Entamoeba* is common in many vertebrate species (Olsen 1974), and several species are parasitic, damaging the intestinal lining of the host (Faust 1975).

Flagellated Protozoan
Fig. 2

From the same bowhead whale (80B7) formalin-fixed colon contents containing an amoeboid protozoan, three flagellates were observed in the material examined. Insufficient specimens were available for species determination. The single-celled organism appeared to be much like a species of *Chilomastix* (Faust et al. 1975) or the "pear"-formed *Hexamita* (Olsen 1974).

Diatoms

Phylum:	Chrysophyta: (Plant Kingdom)
Genera:	*Cocconeis* sp.
	Stauroneis sp.
	Navicula sp.
	Gomphonema sp.

Four genera of diatoms were observed on the epidermis (Figs. 3, 4, 5, 6). Diatoms are plants belonging to the phylum Chrysophyta, which is characterized by silicon cell walls (Fuller and Tippo 1960). They are found in both fresh and salt water and are composed of single cells. There are a large number of diatom species. We observed diatoms on the normal whale epidermis surface and in the eroded areas of the epidermis (Figs. 7, 8, 9). The forms observed on the epidermis surface are common to cetacean hosts (Nemoto 1956, Nemoto et al. 1977, Omura 1950).

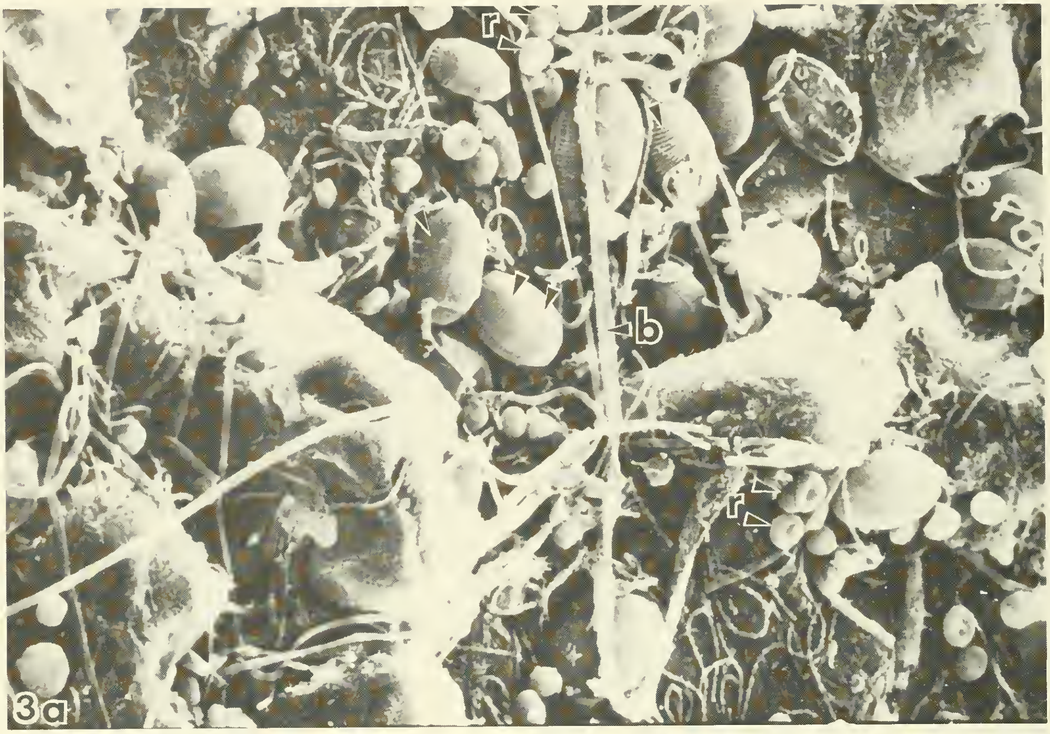


Fig. 3. Scanning electron microscope (SEM) micrographs (3a, 3b) and light microscope micrograph (3c) of one of the most common diatoms, *Cocconeis* (arrowheads), observed during this study. Fig. 3b shows the extent to which *Cocconeis* extends into the epidermis of whale skin. The micron bar at the bottom of each micrograph (SEM) is used to measure object size. Filamentous bacteria (b) and whale red blood cells (r) are present on one micrograph (3a). The light microscope micrograph (3c) is magnified 400X.

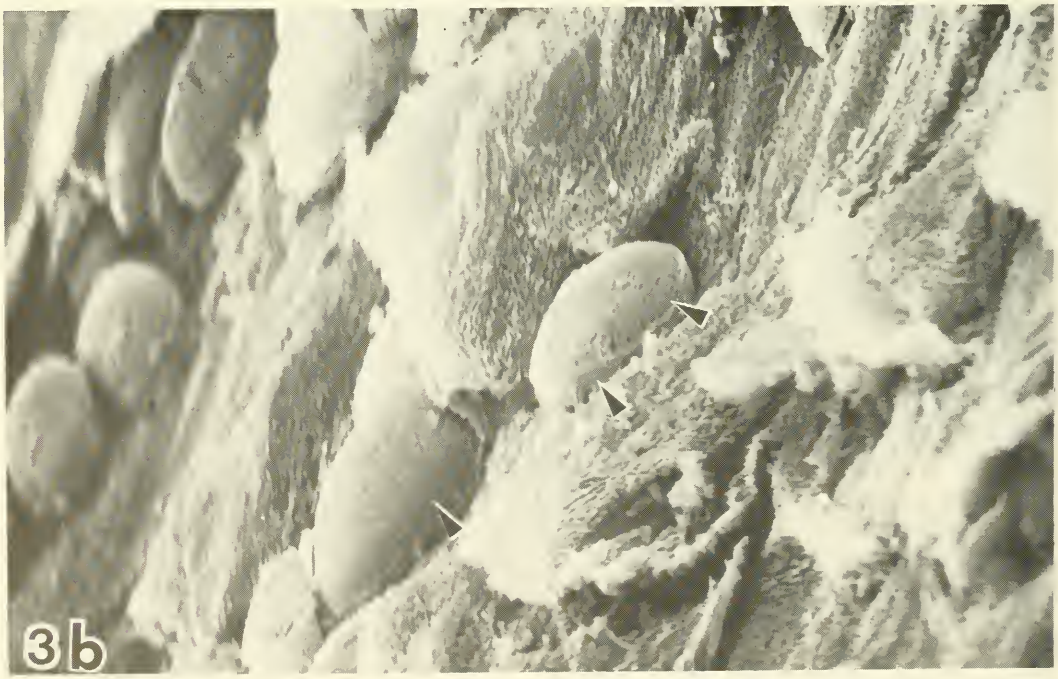


Fig. 3b.

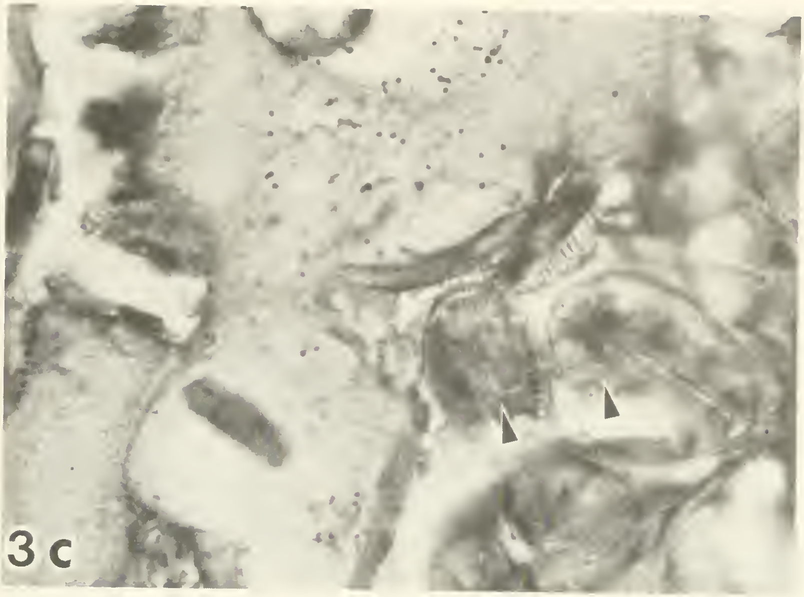
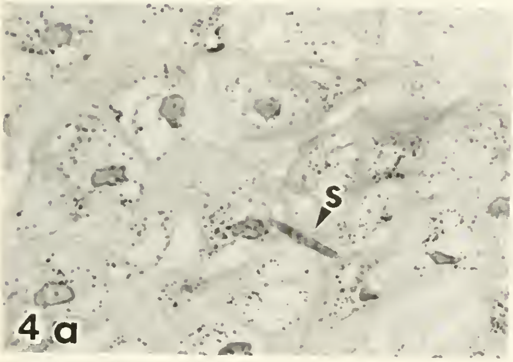


Fig. 3c.



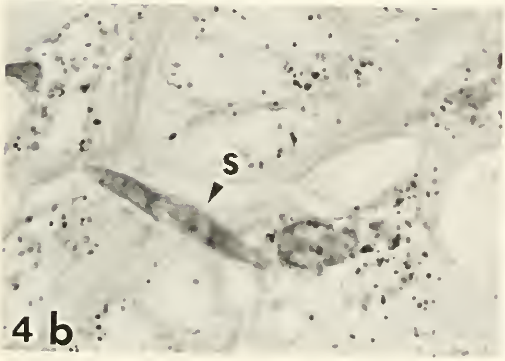


Fig. 4. *Stauroneis* sp. (s) present in a section of bowhead whale epidermis, 4a (400X) and 4b (1,000X).

Helminths

Three species of worms were observed during the examination of whale tissue. One was a digenetic trematode and the other two were roundworms.

Flukes

Phylum:	Platyhelminthes
Class:	Trematoda (Digenea)
Family:	Notocotylidae
Genus, Species:	*Ogmogaster plicatus*

Species of the genus *Ogmogaster* have been reported from both pinnipeds and cetaceans. In the present study 24 specimens were collected from intestinal segments of three bowhead whales (80B2, 80B7, 80B8). Reported in the Antarctic and northern Pacific oceans, these flukes apparently cause no damage to the host (Dailey and Brownell 1972). The anatomy of *O. plicatus* from the bowhead whale was studied and appears to be similar to the antarctic form (Rausch and Fay 1966). The fluke has been reported recently from the bowhead whale (Shults 1979) and has been compared with *O. antarcticus*, *O. trilineatus*, and *O. pentalineatus* (Rausch and Rice 1970). One of the many characteristics for the species of *Ogmogaster* is the number of parallel, lon-

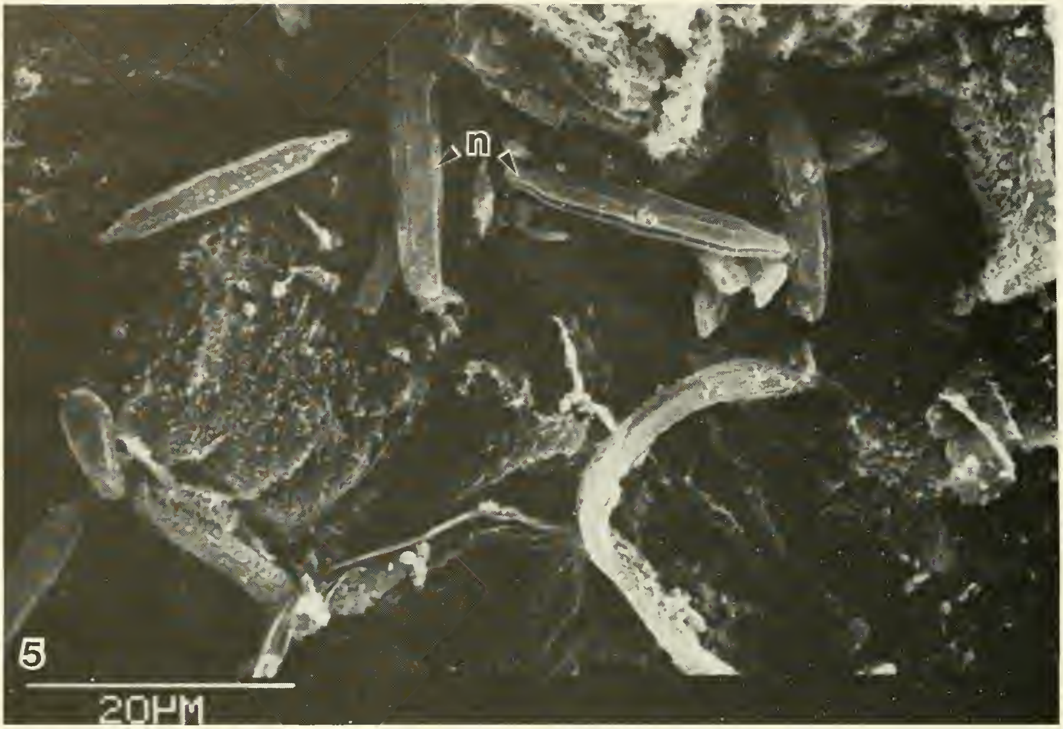


Fig. 5. SEM micrograph of a diatom (n) *Navicula* sp. Note micron bar at bottom of micrograph.

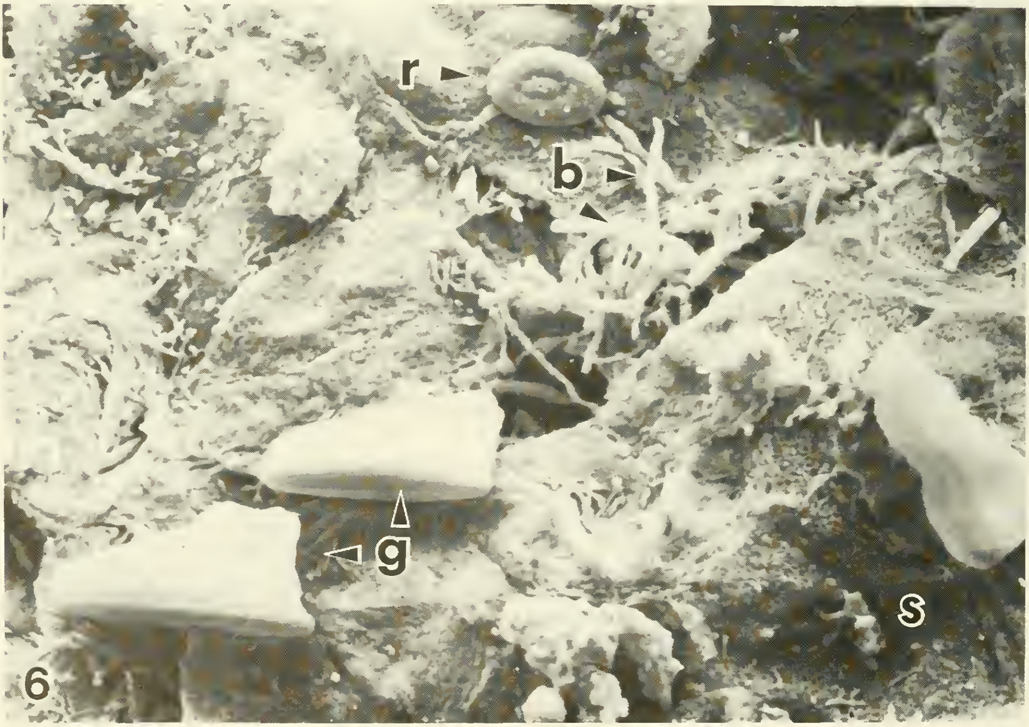


Fig. 6. The diatom (g) *Gomphonema* sp. on the surface of bowhead whale skin(s). Note filamentous bacteria (b) and a biconcave erythrocyte (r) (220X).

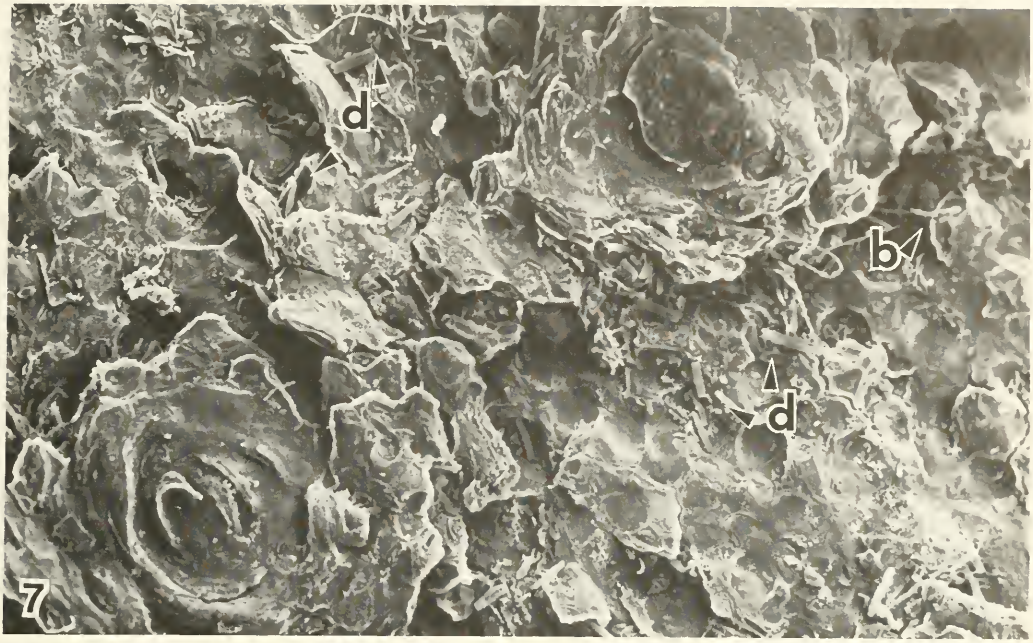


Fig. 7. SEM micrograph of bowhead whale epidermis from an area without prominent erosions of the epidermis. Note filamentous bacteria (b) and diatoms (d) such as *Gomphonema* and *Cocconeis* on the surface of the skin (220X).

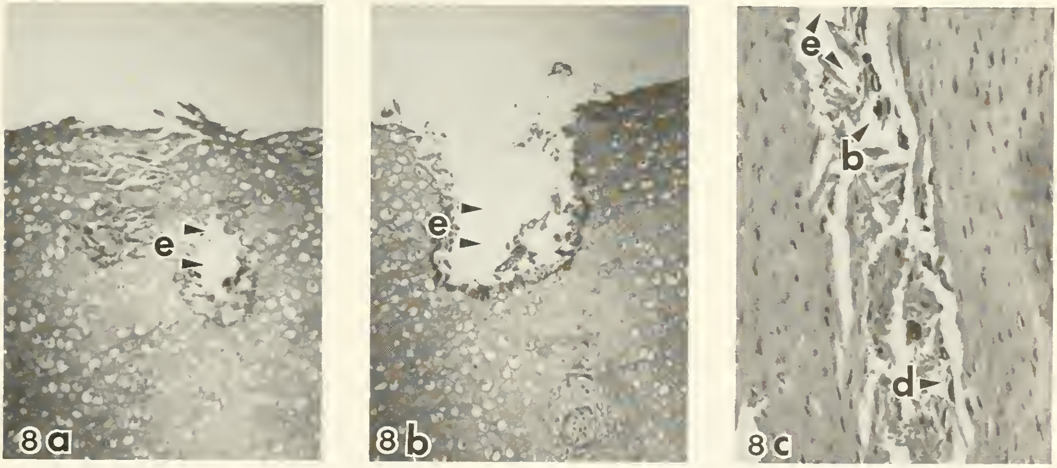


Fig. 8. Bowhead whale epidermis: 8a, the free surface of the skin with initial erosion (100X); 8b (100X) and 8c (400X), the erosion (e) process continuing and the presence of bacteria (b) and diatoms (d) in the eroded area.

gitudinal ridges on the ventral surface. *Ogmogaster plicatus* is characterized by 19–28 ridges with an average of 23 (Rausch and Fay 1966). Figure 10 represents the dorsal and ventral surfaces of *O. plicatus* collected during this study. The life cycle is unknown for this species.

Anisakid-type Larvae

Phylum: Nematoda (The Aschelminthes, Barnes 1980)
Order: Ascaridata
Family: Anisakidae

The piece of bowhead forestomach mounted in paraffin contained larval nematodes that appeared to be an anisakid-type

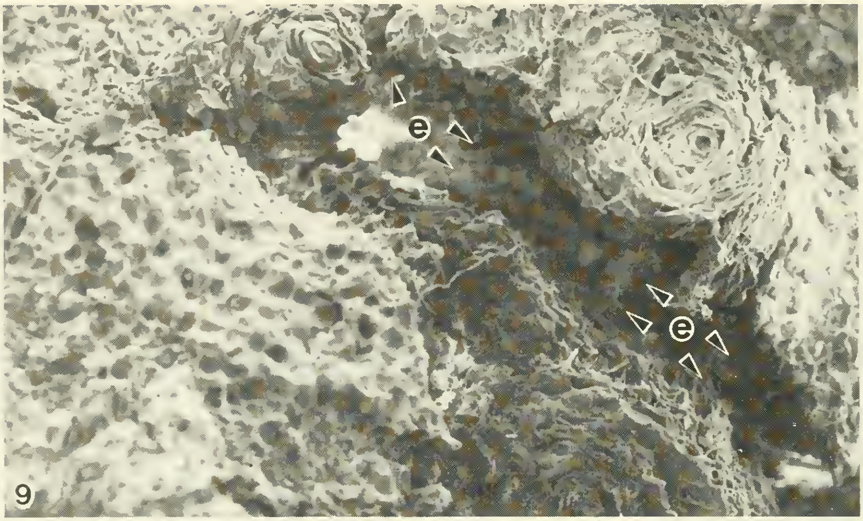


Fig. 9. SEM micrograph representing erosions (e) in the epidermis of whale skin, which usually contains numerous diatoms and bacteria (110X).

larva (Schmidt and Roberts 1984, Migaki et al. 1982) (Fig. 11). No adult stages of this roundworm were observed in examined samples. A description of the life cycle of *Anisakis* is found in parasitology texts (Faust et al. 1975, Schmidt and Roberts 1984) and in recent publications (Smith 1971, Wootten and Waddell 1977, Smith and Wootten 1978, Wootten 1978, Heckmann and Otto 1985). Adult stages of this nematode are characteristically found in stomachs of carnivorous marine mammals (Smith and Wootten 1978). The examined nematode was in the migratory larval phase of its life cycle. Larval characteristics for species of *Anisakis* include: esophagus with a ventriculus that ends obliquely at its junction with the intestine (Hadidjaja et al. 1978), no ventricular appendage nor intestinal caecum, the tail is blunt and terminates in a distinct mucron (Smith and Wootten 1978, Shiraki 1974, Oshima 1972), a prominent boring tooth (mucron) present (Smith and Wootten 1978). For the life cycle of *Anisakis* sp., euphausiids (Crustacea) are probably the most important intermediate host (Smith 1971, Smith and Wootten 1978). Euphausiids are a source of food for the bowhead whale (Lowry and Burns 1979, Lowry and Burns 1980, Lowry and Frost 1984). After examining serial sections of the larval nematode, we noted the following characteristics: no bursa or prominent teeth, blunt tail with mucron remains present, trilobed lips, dentigerous ridge on anterior end, no terminal enlargement for the esophagus, no alae, and overlapping annulations on the surface. The nematode is apparently a species of *Anisakis*. Because we lacked adult worms, which are required for a definitive taxonomic assignment (Smith and Wootten 1978), and because of the taxonomic confusion of the family Anisakidae, the larval nematode will be referred to as "anisakid-type" (Schmidt and Roberts 1984). Yokogawa and Yoshimura (1967) reported larval anisakiasis in the gastrointestinal tract of Japanese people. Recently, cases of anisakiasis have been reported in the United States (Schmidt and Roberts 1984), and larval stages of this roundworm, obtained from salmon harvested at Barrow, Alaska (Heckmann and Otto 1984), were sent to this laboratory.

Anisakid Roundworm

Phylum: Nematoda
Order: Ascaridata

One worm found free in the stomach of animal (80B1) was too poor to evaluate properly; therefore, it is impossible to obtain a complete taxonomic description. This roundworm appears to be *Anisakis* or *Contracaecum*. Members of these genera are among the most common parasites in the stomachs of pinnipeds (Dailey and Brownell 1972).

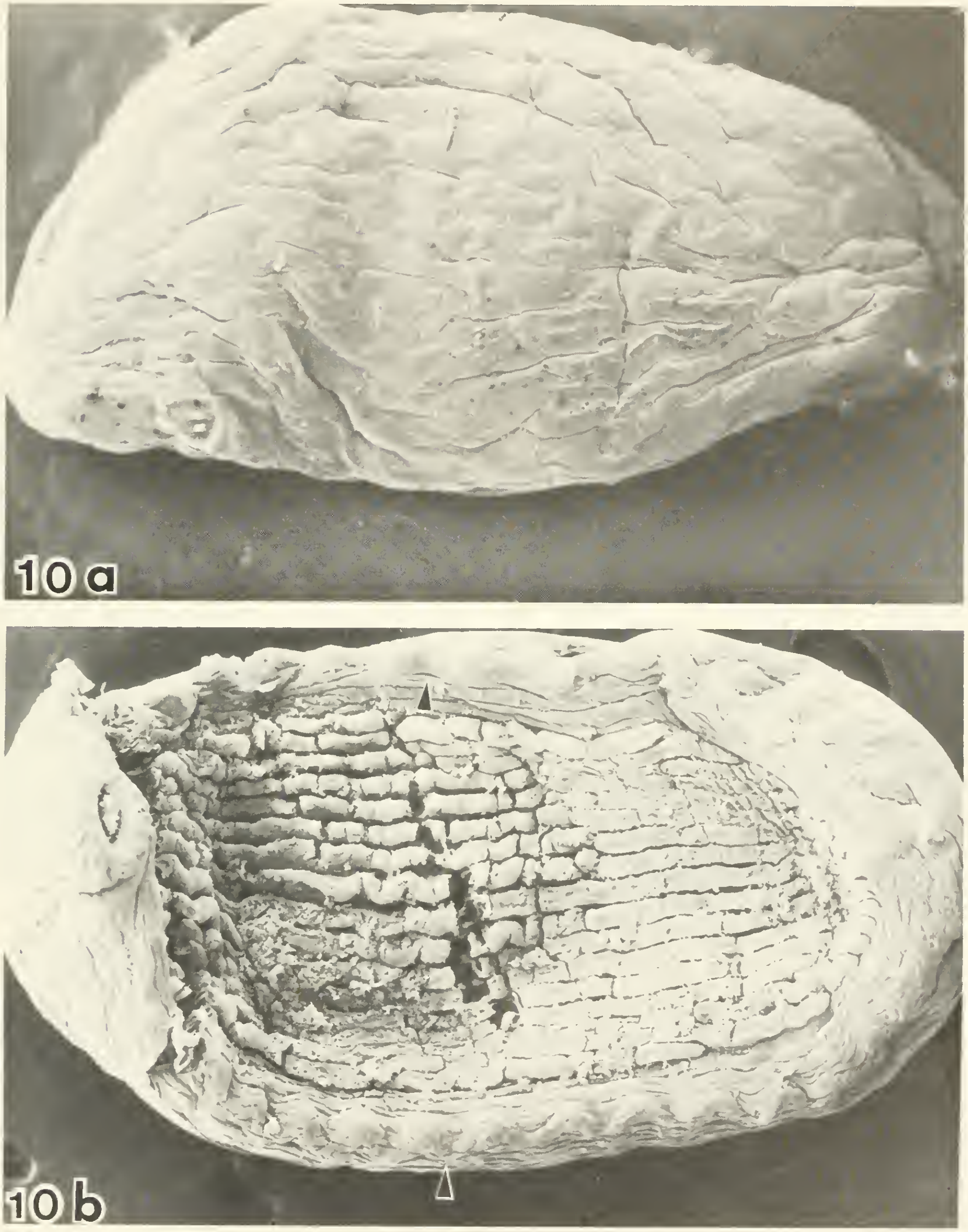


Fig. 10. SEM micrographs of *Ogmogaster plicatus:* 10a, dorsal surface of the trematode (18X); 10b, ventral surface (25X). Note the characteristic lateral varigations (arrowheads) for this species and the longitudinal ridges on the ventral surface.

Whale Lice

Phylum: Arthropoda
Class: Crustacea
Order: Amphipoda
Genus, Species: *Cyamus ceti*, highly modified for a parasitic mode of life

Cyamids have a vestigial abdomen, but the body, an exception among amphipods, is broad, depressed, and bears large legs (Leung 1967). The cyamids of whales have a high degree of host specificity; however, the same species that occurs on the bowhead whale is

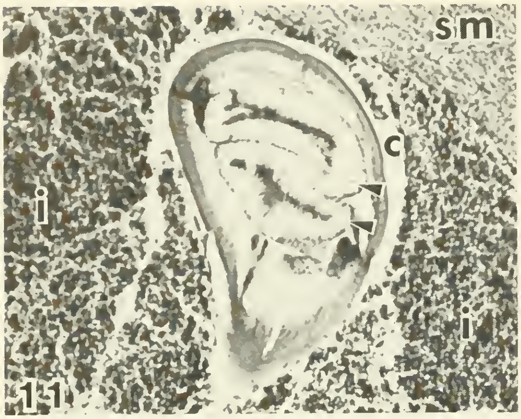


Fig. 11. The larval anisakid-type roundworm (arrowheads) found encysted (c) in the submucosa (sm) of the bowhead whale forestomach. Note the inflammatory (i) response around the nematode (100X).

found on gray whales. The species *Cyamus ceti* is one of the most common parasites observed during this and a previous study (Heckmann et al. 1980, Heckmann 1981).

Figure 12 represents the ventral surface of a whale louse. Note the enlarged appendages with numerous hooks. The mouthparts, as well as the appendages, are highly modified for the ectoparasitic mode of life. The cyamids have a direct life history with the young whale lice being released from the broodpouch of the female. The amphipods have no free-swimming stage. Subsequent moultings produce sexually mature adults.

Other Reported *Balaena mysticetus* Parasites

NEMATODE.—*Crassicauda crassicauda* is a nematode parasitizing the urogenital system and sometimes other parts of the body. Although the life cycle of *C. crassicauda* has not been determined, members of the order in which this genus belongs reproduce viviparously or ovoviparously and parasitize the body cavity, blood sinus, air bladder, or other tissues of aquatic vertebrates. Copepods are considered intermediate hosts for *C. crassicauda*. For cetaceans, the nematode has been reported from *Tursiops truncatus* (bottlenosed dolphin), *Balaenoptera musculus* (blue whale), *Megaptera novaengliae* (humpback whale), *Balaen mysticetus* (bowhead whale), *Ziphius cavirostris* (Cuvier's beaked whale), *Balaenoptera acutorostrata* (minke whale), *Balaenoptera borealis* (sei whale), and *Balaenoptera physalus* (fin whale) (Dailey and Brownell 1972).

TREMATODE.—*Lecithodesmus goliath* is a fluke that parasitizes bile ducts of Cetacea. *Lecithodesmus goliath* produces large eggs that are triangular in cross-section. Molluscans are intermediate hosts, and metacercariae can be ingested with the molluscan intermediate host (Dailey and Brownell 1972). Small clams (bivalves), which are members of the phylum mollusca, have been reported from the colon of a bowhead whale (Lowry and Burns 1979).

ACANTHOCEPHALA.—*Bolbosoma balaenae* is an acanthocephalan that is found in the intestine of marine mammals including *B. mysticetus* (Dailey and Brownell 1972, Neiland 1962).

The parasites observed during this study and all those reported for the bowhead whale are listed in Table 3. The parasites reported for the bowhead whale are compared with those reported for two other cetaceans, the gray whale (*Eschrichtus robustus*) and the blue whale (*Balaenoptera musculus*)(Table 4).

DISCUSSION

Samples of bowhead whale tissue were sent to our laboratory during 1980 to be examined for parasites. From samples of five bowhead whales, two protozoans, four genera of diatoms, and a nematode have been added to the existing list of parasites (Table 3). With additional samples, the list would most likely be expanded, especially the protozoan forms. Data from this study confirmed the presence of *Cyamus ceti*, a whale louse, as well as the presence of an *Ogmogaster*, which had been described in a bowhead whale in 1979 (Shults 1979). Samples of blood from four whales were negative for parasites.

Because of its currently known dietary habits, the bowhead whale is not subject to many of the internal parasites found in marine mammals that feed on fish, large crustaceans, and mollusks. Fish, large crustaceans, and mollusks are common intermediate hosts for helminths of marine mammals (Ridgway and Dailey 1972).

The bases for placing the protozoan, found in the colon contents of one whale, in the family Endamoebidae are its small size and location, the presence of one to four nuclei per

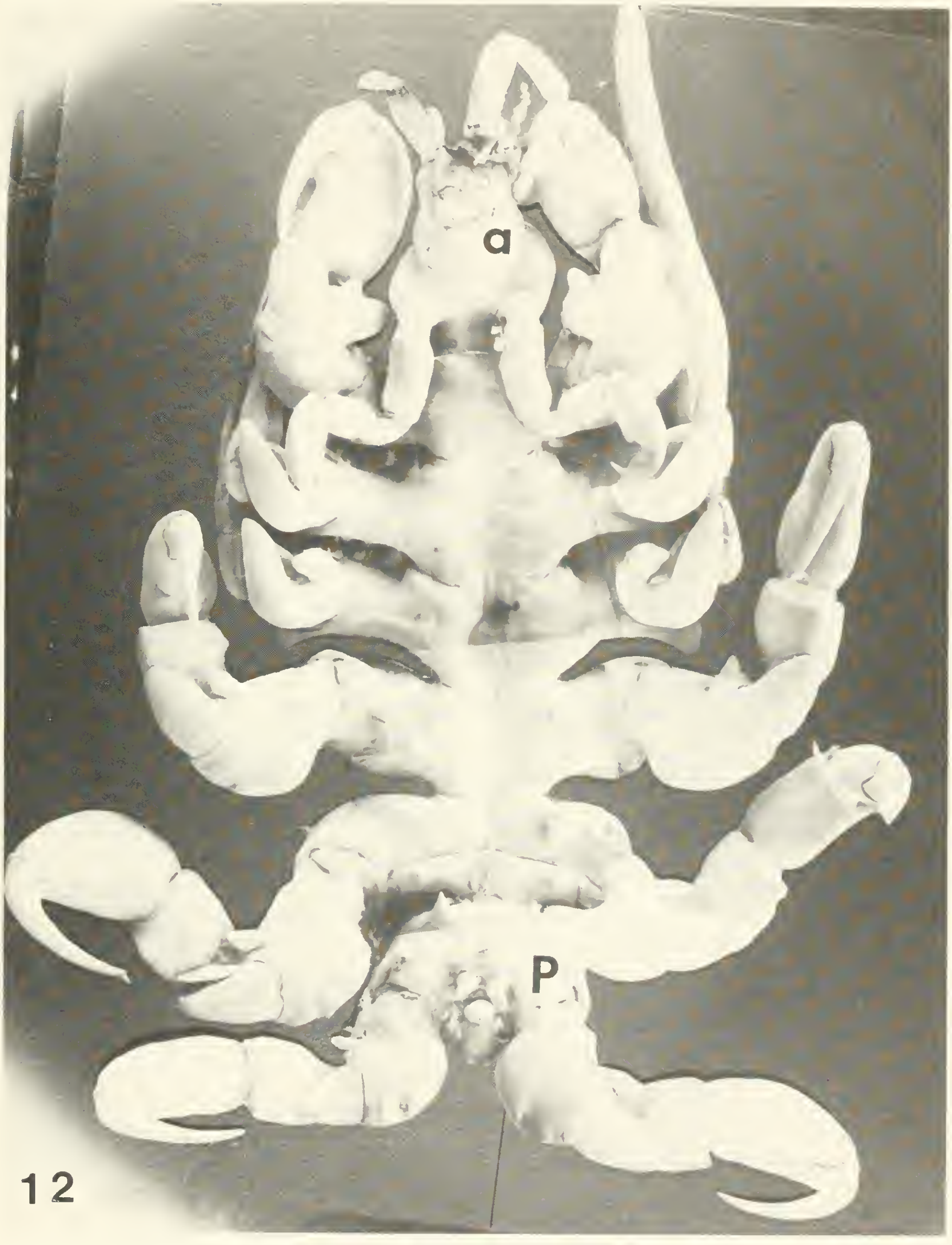


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Fig. 12. SEM of the ventral surface of the whale "louse," *Cyamus ceti* (8X). *Cyamus ceti* is not a louse but a highly modified amphipod infesting the skin of whales. The anterior (a) and posterior (p) parts of *C. ceti* are labeled.

cyst, and numerous food vacuoles in the cytoplasm. Members of the Endamoebidae are typically parasites or commensals of the digestive systems of arthropods and vertebrates (Schmidt and Roberts 1984). Species of *Entamoeba* are common entocommensals and parasites of the digestive system of vertebrate and invertebrate hosts. The present study is the first record of a protozoan parasite for the bowhead whale. Additional material must be

TABLE 3. A consolidated list of parasites for *Balaena mysticetus*, bowhead whale.

Parasite	Location in host
Protozoa	
*Amoeba form *Entamoeba* sp.	Colon, small intestine
*Flagellate form	Colon, small intestine
Diatoms: (Plant)	
**Cocconeis*	Skin, normal and eroded areas
**Stauroneis*	
**Navicula*	
**Gomphonema*	
Acanthocephala	
***Bolbosoma balaenae*	Intestine
Cestoda (Platyhelminthes)	
***Phyllobothrium delphini*	Tissue (blubber)
Trematoda (Platyhelminthes)	
**Ogmogaster plicatus*	Intestine
***Lecithodesmus goliath*	Bile ducts
Nematoda	
*Anisakis-type larvae	Forestomach submucosa, encysted
*Anisakid: *Contracaecum* or *Anisakis*	Stomach
***Crassicauda crassicauda*	Intestine
Amphipoda	
**Cyamus ceti*	Attached to baleen

*Parasites observed during this study.
**Parasites not observed during this study, but reported for the bowhead whale (Dailey and Brownell 1972).

collected from the colon of *Balaena mysticetus* to determine the characteristics of this flagellated protozoan and its correct taxonomic status. Only three examples of the flagellate were observed from material taken during 1980.

The ideal situation for examining tissue for parasites is to be "on site" when an animal is killed. The necessity for examining tissue from the brain and ear, which was not available for this study, is due to the implication of two helminths in whale strandings (Stroud and Dailey 1978, Ridgway and Dailey 1972, Stroud and Roffe 1979). The trematode *Nasitrema* infects the central nervous system, and a species of *Stenurus*, a nematode, has been found in the ears of cetaceans. The brains of stranded animals have shown parasitically induced lesions caused by trematode (*Nasitrema*) eggs. Parasites may be a partial explanation for cetacean strandings (Beverly-Burton 1978).

Presumably due to feeding habits of the host (Lowry and Burns 1980, Lowry and Frost 1984, Lowry et al. 1978), no adult tapeworms have been reported for the bowhead whale. *Phyllobothrium delphini* is a cestode larval stage (plerocercoid) found in the blubber of whales, usually around the anal orifice (Dailey and Brownell 1972). We did not find cestode plerocercoids in the samples of bowhead whale tissue sent to us for this study.

Diatoms are common organisms attached to the skin of whales (Nemoto 1956). Numerous diatoms, single-celled plants containing silicon walls, were observed infesting the skin of bowhead whales from 1980 skin samples. Four genera were identified in the present study. Diatoms were 5 to 10 times more numerous in the eroded areas of the host's skin than in noneroded areas; bacteria and protozoa were also found in the same erosions. The skin of cetacea is an important area for thermoregulation (Ridgway 1972). Japanese workers consider diatoms to be parasitic on whale skin (Nemoto 1977, Omuro 1950). Once an opening is established in the outer surface of the skin, diatoms, bacteria, and protozoa (Figs. 13, 14) may become opportunists and use this area as a microhabitat. Excessive numbers of such opportunists appear to damage the skin.

The nematode *Anisakis* is common in marine mammals (Dailey and Brownell 1972). Larval anisakids have been reported in the digestive tract of humans (anisakiasis), and in Europe and Japan there are records of this helminth as a possible cause of host death (Faust 1975, Schmidt and Roberts 1984). A limited number of cases of anisakiasis have been reported in North America (Myers 1979, Dailey et al. 1981). Fish samples sent to our laboratory from Alaska contained a larval anisakid (Heckmann and Otto 1985).

Including the results of the present study, two protozoans, four diatoms, two trematodes, one cestode, one acanthocephalan, two nematodes, and one amphipod (louse) represent the current list of parasites for the bowhead whale.

ACKNOWLEDGMENTS

We thank the on-site tissue-collection team at Barrow, Alaska, under the direction of Dr. Thomas F. Albert, for assistance in collection of specimen material. We also thank James Allen and Connie Swenson, Brigham Young University Electron Optics Laboratory, who assisted with the SEM preparations. Dr. Jer-

TABLE 4. Comparison of parasites observed in three species of baleen whales.

	Parasite group with listed species																					
	Protozoa			Acanthocephala					Cestoda*				Trematoda*				Nematoda					Amphipoda**
Baleen whale (host)	E	F	D	B_1	B_2	B_3	B_4	C	P_1	P_2	P_3	T	O_1	O_2	O_3	L	A	A_1	C_1	C_2	P	C
Eschrichtus robustus[1] Gray whale	O	O	O	O	O	O	O	P	O	P	P	O	O	P	P	O	O	O	O	O	O	O
Balaenoptera musculus[2] Blue whale	O	O	O	P	P	P	P	O	O	P	O	P	P	P	O	O	P	O	P	O	P	P
Balaena mysticetus[3]	P	P	P	P	O	O	O	O	P	O	O	O	P	P	O	P	O	P	P	P	O	P

O -Not observed
P=Observed in host
*Phylum. Platyhelminthes
**Phylnm. Arthropoda
[1,2]Dailey and Brownell 1972
[3]This study and Dailey and Brownell 1972

Codes for parasites.

Protozoa
E — Amoeboid form (*Entamodeba*)
F — Flagellate
D — Diatoms. 4 species

Acanthocephala
B_1 — *Bolbosoma balaenae*
B_2 — *Bolbosoma brevicolle*
B_3 — *Bolbosoma hamiltoni*
B_4 — *Bolbosoma turbinella*
C — *Corynosoma* sp.

Cestoda
P_1 — *Phyllobothrium delphini*
P_2 — *Priapocephalus* sp.
P_3 — *Pseudophyllidae* sp.
T — *Tetrabothrius affinis*

Trematoda
O_1 — *Ogmogaster plicatus*
O_2 — *Ogmogaster antarcticus*
O_3 — *Ogmogaster pentalineatus*
L — *Lecithodesmus goliath*

Nematoda
A — *Anisakis*
A_1 — Anisakis-type larvae
C_1 — *Crassicauda crassicauda*
C_2 — *Contracaecum* sp.
P — *Porrocaecum decipiens*

Amphipoda
C — *Cyamus ceti*

rold T. Haldiman, Louisiana State University, provided Figures 3a, 5, and 14 for this report. This study was supported by Bureau of Land Management Contract AA851-CT0-22 to the University of Maryland, College Park, Maryland.

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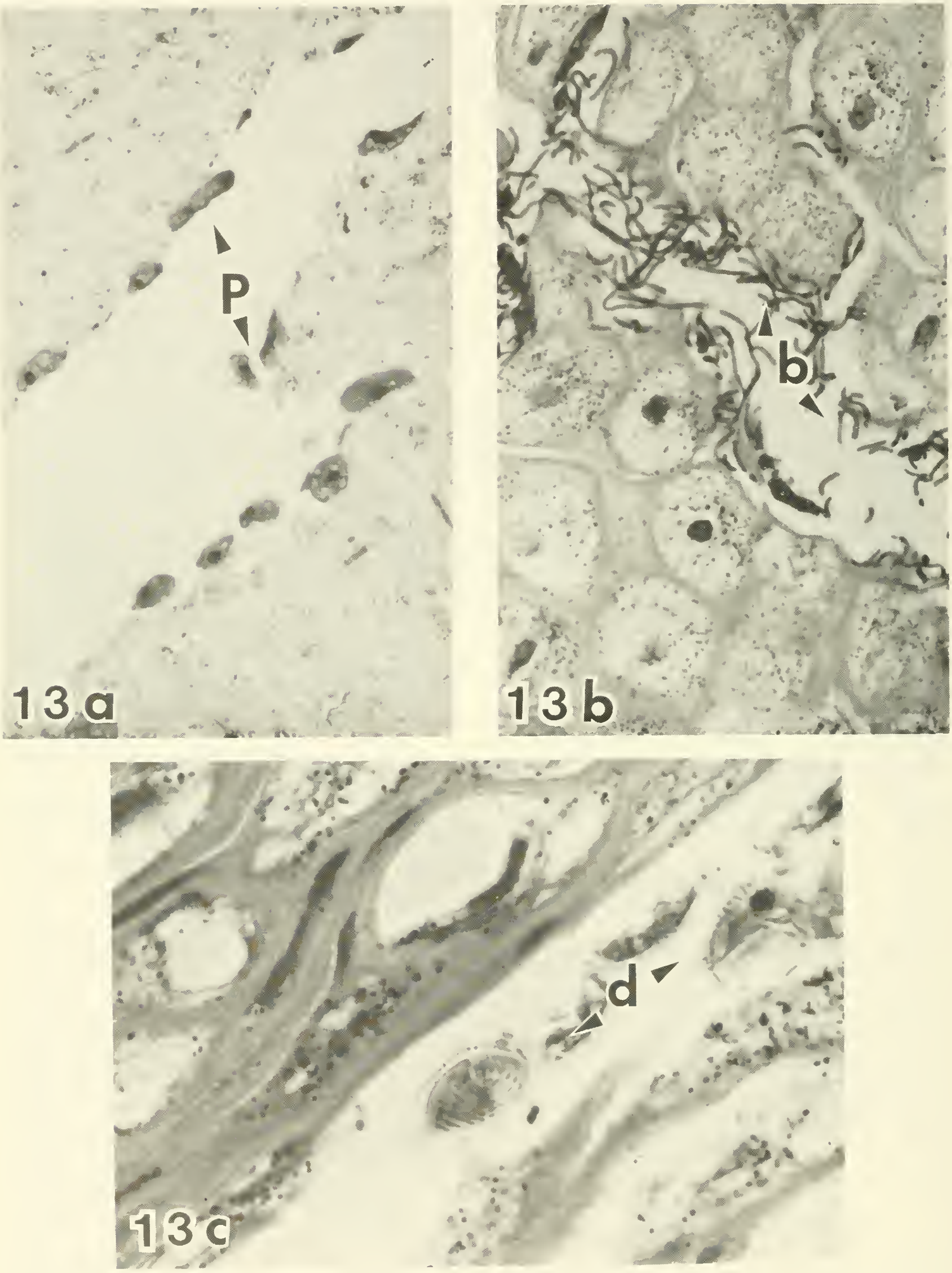

Fig. 13. Micrographs representing the presence of: 13a, protozoa (P); 13b, bacteria (b); and 13c, diatoms (d) in the eroded areas of bowhead whale epidermis (1,000X).

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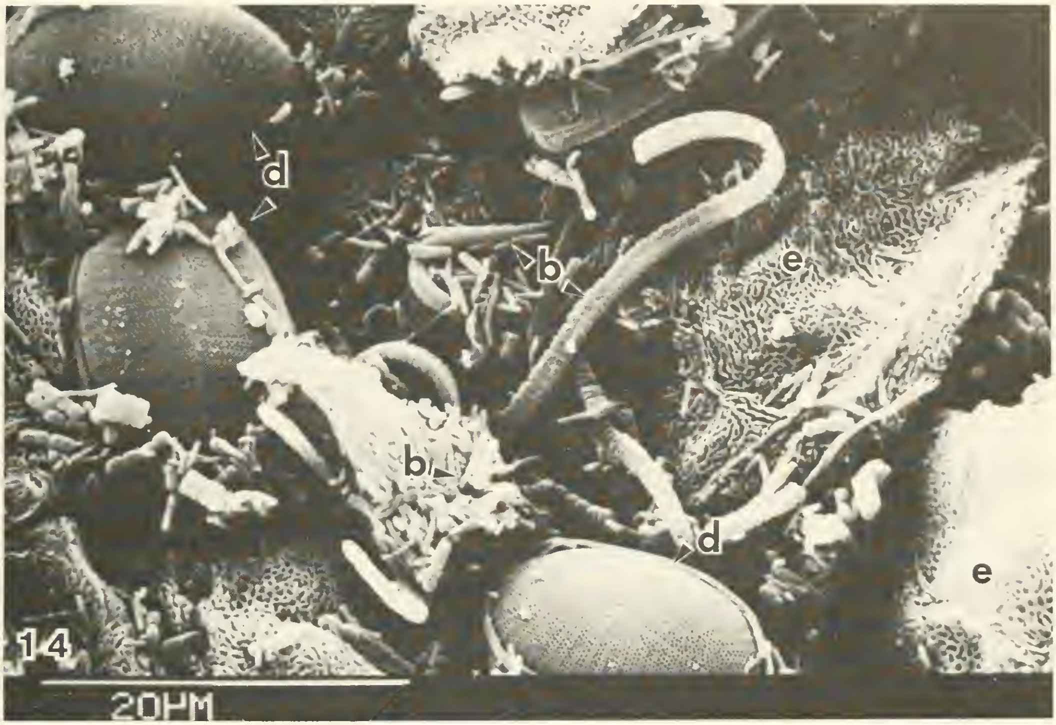

Fig. 14. SEM micrograph of bowhead whale skin representing the types of organisms, bacteria (b) and diatoms (d), that could invade erosions in the host epidermis (e). Note micron bar.

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REPRODUCTION OF THE PRAIRIE SKINK, *EUMECES SEPTENTRIONALIS*, IN NEBRASKA

Louis A. Somma[1]

ABSTRACT.—Clutch sizes of the prairie skink, *Eumeces septentrionalis*, in Nebraska are positively correlated with female snout-vent lengths (SVLs). Data presented in this study and others indicate Nebraska populations of *E. septentrionalis* have larger average clutch sizes than other populations within this species' range.

The prairie skink, *Eumeces septentrionalis*, is a semi-fossorial, oviparous lizard inhabiting the central lowland province region and tall-grass prairies of North America (Breckenridge 1943, Nelson 1963). In Nebraska, *E. septentrionalis* is found primarily in tall-grass prairies (Lynch 1985) and urban habitat (Somma 1985a). Few reproductive data exist for Nebraska populations (Gehlbach and Collette 1959, Iverson 1976, Somma 1985b). This study summarizes data on clutch size and SVL of 21 captive female *E. septentrionalis* collected in eastern Nebraska.

TABLE 1. Female SVL, clutch size, and mean egg dimension for *Eumeces septentrionalis*.

SVL (cm)	Clutch size	Mean egg dimension (length x diameter cm)
7.88	18	1.26 × 0.81
6.96	7	1.31 × 0.86
7.42	11	1.27 × 0.76
6.96	13	1.15 × 0.69
6.30	4	**
6.74	7*	**
7.48	11	1.08 × 0.72
6.77	4	1.21 × 0.72
6.64	6	1.18 × 0.74
8.00	13	1.20 × 0.71
7.14	11	1.32 × 0.85
6.96	8	1.23 × 0.80
7.28	12	1.19 × 0.74
7.98	17	1.05 × 0.71
8.04	17	1.14 × 0.81
7.38	11	1.09 × 0.76
6.96	13	1.21 × 0.73
7.48	11	1.04 × 0.82
6.82	11	1.05 × 0.77
7.50	13	1.04 × 0.78
7.32	12	**

*oviducal egg count
**not obtained

Eighteen gravid females from Douglas County and three from Pawnee County were collected in May 1984 and placed in separate plastic terraria containing a moist soil substrate. Each terrarium contained a 15 × 15-cm acrylic plate under which the skinks could oviposite. The skinks were fed crickets and mealworms *ad libitum*. A 14L:10D photoperiod was maintained for the duration of the study.

Oviposition occurred between 18 and 30 June, and the eggs were brooded by the females. Measurements of initial egg dimensions were obtained for each clutch (Table 1). An egg that was removed from one clutch immediately upon oviposition contained an embryo in an advanced stage (32–33) of development (Dufaure and Hubert 1961). One female died before ovipositing and was found to contain 7 oviducal eggs that were included in the analysis. The mean clutch size was 10.95 ± 0.85 eggs (range = 4–18). A linear regression (Sokal and Rohlf 1981) indicates that clutch size has a highly significant positive correlation with female SVL (Fig. 1, $r^2 = 0.706$, $P < .0001$). Clutch sizes for other populations of *Eumeces septentrionalis* are as follows: Minnesota, $\bar{x} = 8.79$, $N = 19$ (Breckenridge 1943), $\bar{x} = 6.60$, $N = 9$ (Nelson 1963); Wisconsin, 4–6, $N = 3$ (Vogt 1981); Nebraska, $\bar{x} = 14.5$, $N = 2$ (Gehlbach and Collette 1959), $\bar{x} = 14.0$, $N = 5$ (Iverson 1976), $\bar{x} = 14.7$, $N = 3$ (Somma 1985b); Kansas, $\bar{x} = 8.00$, $N = 4$ (Clarke 1955); Texas, 9, $N = 1$ (Smith and Slater 1949), 9, $N = 1$ (Sabath and Worthington 1959).

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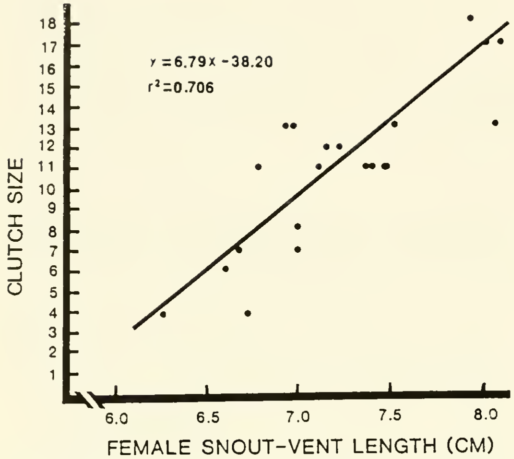

Fig. 1. Regression plot of clutch size vs. female SVL for *Eumeces septentrionalis*.

Fitch (1985) has summarized clutch size data for *Eumeces septentrionalis* using previously published data. Populations were described as "northern" (Breckenridge 1943) or "southern" (Clarke 1955, Gehlbach and Collette 1959, Sabath and Worthington 1959, Iverson 1976) and were combined to obtain a mean for "northern" populations and another larger mean representing "southern" populations (Fitch 1985). These data were used to illustrate a north-south trend in increasing clutch size within this lizard's range. Listing Nebraska and Kansas populations as southern, however, is inappropriate and results in an unnaturally large mean. Earlier studies suggesting that Nebraska populations of *E. septentrionalis* have larger clutch sizes than others to the northern and southern ends of its range (Gehlbach and Collette 1959, Iverson 1976) are supported by this study. Mean clutch sizes in these previous studies, however, could have been exaggerated by the limited sample sizes. Larger samples obtained from other populations throughout this species range, along with corresponding SVL data, would greatly facilitate comparisons of reproductive data.

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LIST OF IDAHO SCOLYTIDAE (COLEOPTERA) AND NOTES ON NEW RECORDS[1]

Malcolm M. Furniss[2] and James B. Johnson[2]

ABSTRACT.—Reported are 105 species of Scolytidae (Coleoptera) from Idaho. About one-third of these are rarely collected, of which 22 species are known from a single locality each. Twelve species reported from Idaho for the first time are: *Carphoborus carri* Swaine, *C. sansoni* Swaine, *Phloeosinus hoferi* Blackman, *Conophthorus monophyllae* Hopkins, *Dryocoetes betulae* Hopkins, *Ips confusus* (LeConte), *Pityophthorus absonus* Blackman, *P. aquilus* Blackman, *P. blandus* Blackman, *P. deletus* LeConte, *P. scalptor* Blackman, and *Xyleborinus saxeseni* (Ratzeburg). Significant extensions of the known distributions in Idaho are reported for seven other scolytids: *Alniphagus aspericollis* (LeConte), *Dendroctonus murrayanae* Hopkins, *Phloeotribus lecontei* Schedl, *Procryphalus mucronatus* (LeConte), *Trypophloeus populi* Hopkins, *Xyleborus dispar* (Fabricius), and *X. intrusus* Blandford. *Xyleborus dispar* especially needs study in anticipation that it may become increasingly important in Idaho fruit trees and other woody plants including ornamentals and shade trees.

Idaho has an abundance of trees and shrubs that can serve as scolytid hosts, but the scolytids of Idaho have not been surveyed systematically to determine the total number of species, their specific hosts, and their distributions within the state. Such information is fundamental to the orderly development of the natural history of this region and will facilitate scolytid research. For example, the genus *Dendroctonus* contains several of our most abundant and destructive species (e.g., *D. ponderosae* Hopkins) and one of the least abundant and least destructive (*D. murrayanae* Hopkins). By knowing where *D. murrayanae* occurs, it can be studied and the circumstances that keep it from becoming abundant may prove important in managing species that are sometimes damaging.

Since 1984 we have compiled a comprehensive list of Idaho scolytids from literature, museum specimens, and our own field collections. This task was stimulated by the recent availability of the works of R. L. Furniss and V. M. Carolin (1977), D. E. Bright, Jr. (1981), and, especially, S. L. Wood's monograph on North American bark and ambrosia beetles (1982).

Twenty-two Idaho species are represented by only single specimens or localities. Additional species doubtless occur in Idaho but have not yet been found or reported, and some exotic species may find their way here in the future, either to settle quietly into their new niches or to attain importance in ornamentals, fruit trees, or forests. So, the list will likely change as our work continues.

Besides the list of 105 species and their abundance, we present notes on 12 species reported from Idaho for the first time and major range extensions within Idaho for 7 other species. All measurements of host material are in metric units, including distances from landmarks, although the latter are invariably in miles on labels of pinned museum specimens. Names of collectors are given as per labels or as stated in the literature. The numbers of known pinned adult specimens follow the collection data. Specimens deposited in the University of Idaho, William F. Barr Entomological Museum, are designated UI-WFBM. Known repositories of others are abbreviated as follows: SLW = S. L. Wood Collection, Brigham Young University, Provo, Utah; WSU = Washington State University, Pullman, Washington; CNC = Canadian National Collection, Ottawa, Ontario, Canada. In other cases, we cite the literature from which we acquired the record.

SPECIES NEW TO IDAHO

Subfamily Hylesininae

Carphoborus carri Swaine

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Type locality: Edmonton, Alta., Canada. Biology: Unstudied. Polygynous; breeds in relatively dry, dead bark of boles of small, suppressed spruces and unthrifty, lower branches of living trees. Galleries deeply score the wood (Wood 1982). Distribution and notes: CANADA: Alta., Man., New Brun., NWT, Yuk.; USA: Alas., Mont., S. Dak., Wyo., IDAHO: North shore of Henrys Lake, Fremont Co., 21-VII-1985, *Picea glauca*, M. M. Furniss and J. B. Johnson (19 ♀, 17 ♂ UI-WFBM). A southernmost population of white spruce, *Picea glauca* (Moench) Voss, grows on boggy ground along the north shore of Henrys Lake. The trees may be hybrids of white and Engelmann spruce. Five *C. carri* new adults were taken from a lower branch of a recently dead, standing tree that was 50 cm diameter and 37 m tall.

Carphoborus sansoni Swaine

Type locality: Banff, Alta., Canada. Biology: Unstudied. Polygynous; breeds in bark of the bole of unthrifty, suppressed seedlings and in unthrifty, shaded-out branches of large, living, standing trees (Wood 1982). Distribution and notes: CANADA: Alta.; USA: Colo., Ore., Ut., Wyo., IDAHO: Emigration Campground, 24 km W of Montpelier, Bear Lake Co., 24-VII-1984, *Picea engelmannii*, M. M. Furniss and J. B. Johnson. (1 UI-WFBM). Collected from a shaded-out limb on a wind-thrown tree.

Phloeosinus hoferi Blackman

Type locality: Ute Pass, Colo. Biology: Unstudied. Monogynous. Infests bark of small branches and twigs of dying trees (Wood 1982). Distribution and notes: CANADA: B.C.; USA: Ariz., Calif., Colo., Nev., N.M., N.Dak., S.Dak., Tex., Ut., Wyo., IDAHO: Two km N of Almo, Cassia Co., 25-VII-1984, *Juniperus osteosperma*, M. M. Furniss and J. B. Johnson (1 UI-WFBM). Reared from a 23-cm-diameter felled, limbed tree; probably emerged from branches 2–10 cm diameter. At time of collection (25-VII-1984), mature larvae and pupae were present, but these may have been exclusively *P. serratus* LeConte, a larger species that was abundant, especially in the trunk.

Subfamily Scolytinae

Conophthorus monophyllae Hopkins

Type locality: Ventura Co., Calif. Biology: Unstudied. In other studied species, the female bores into the cone base in spring at the beginning of the second year of cone growth. The egg gallery extends the length of the cone center. Progeny mature during that summer within the cone and generally overwinter there, although in the case of *C. ponderosae* Hopkins (= *C. lambertianae* Hopkins), some adults emerge in the fall and overwinter in the tips of live twigs (R. L. Furniss and V. M. Carolin 1977). Distribution and notes: Calif., Nev., Ut., IDAHO: City of Rocks, Cassia Co., 25-VII-1984, *Pinus monophylla* cones, M. M. Furniss and J. B. Johnson (12 UI-WBFM, 5 SLW). Attacked cones common, most contained a single beetle, mired and dead in profuse resin exuded from entrance located at base of cone (i.e., often unsuccessful).

Dryocoetes betulae Hopkins

Type locality: Grant Co., Va. Biology: Unstudied. Polygynous. It infests bark of stumps and the bole and limbs of recently cut and unthrifty trees (Wood 1982). Distribution and notes: CANADA: Alta., B.C., Newf., N.B., Ont., Que.; USA: D.C., Fla., La., Me., Mich., Miss., Mont., N.H., N.J., N.Y., Calif., Penn., Va., V.I., Vt., W.Va., Wash., IDAHO: Reeder Bay, Priest Lake, Bonner Co., 6-VIII-1985, *Betula papyrifera*, M. M. Furniss, J. B. Johnson, and S. J. Gast (13 UI-WFBM). Parents, larvae, and one pupa in phloem of the trunk of a 46-cm-diameter tree toppled by snow in previous winter. Sporadic infestation also noted in 15-cm-diameter basal portion of a tree that had broken off at 3 m height.

Ips confusus (LeConte)

Type locality: Southern Calif. Biology: Polygynous. Three to four generations per year reported in southwestern states (fewer likely in Idaho). Adults may overwinter en masse under bark of main stem, thoroughly scoring the wood surface (Chansler 1964). Distribution and notes: MEXICO: Baja Calif., Chih.; USA: Ariz., Calif., Colo., Nev., N.M., Ut., Tex., (Wyo.), IDAHO: City of Rocks, Cassia Co., *Pinus monophylla*, 14-VI-

1968, W. F. Barr (2 UI-WFBM); same locality, 25-VII-1984, M. M. Furniss and J. B. Johnson (4 UI-WFBM, 3 SLW). Mainly teneral, but some darkened, adults in base of a dead 23-cm-diameter standing tree with bright orange foliage. Some *Pityophthorus* intermingled; *Dendroctonus valens* LeConte and *Hylurgops porosus* LeConte below.

Pityophthorus absonus Blackman

TYPE LOCALITY: Mineral King, Calif. BIOLOGY: Unstudied. Polygynous. Reported fairly common at high elevation (Bright 1981) and infesting small branches and in shaded-out small trees (Wood 1982). DISTRIBUTION AND NOTES: CANADA: Alta., B.C.; USA: Calif., Colo., Mont., Nev., Ut., IDAHO: 16 km E of Wayan, Caribou Co., 21-VII-1984, *Abies lasiocarpa*, M. M. Furniss and J. B. Johnson (9 UI-WFBM, 2 CNC). Attacking shaded-out, 1–2-cm-diameter branches. Eight km S of Old Williamsburg, Caribou Co., 22-VII-1984, *Abies lasiocarpa*, M. M. Furniss and J. B. Johnson (1 UI-WFBM, CNC). Reared from larvae infesting green 0.5–3.5-cm-diameter branches on ground. Six km E of Bostetler Guard Station, Cassia Co., 26-VII-1985, *Abies lasiocarpa*, M. M. Furniss and J. B. Johnson (1 UI-WFBM). Parent beetles from current-year attacks in 0.8–2.0-cm-diameter branches of 30-cm-basal-diameter dead tree with red foliage. Salmon Mtn., Idaho Co., 18-VII-1985, *Abies lasiocarpa*, M. M. Furniss and J. B. Johnson (8 UI-WFBM). Top-killed, 10-cm-diameter, 5-m-tall tree.

Pityophthorus aquilus Blackman

TYPE LOCALITY: Kaibab National Forest, Ariz. BIOLOGY: Polygynous. Infests lateral branches of lodgepole pine in association with the weevil, *Pissodes terminalis* Hopping (Colo.). Attack and emergence occur in midsummer (Bright 1981). DISTRIBUTION AND NOTES: CANADA: Alta., B.C., Sask; USA: Ariz., Calif., Colo., Mont., N.M., S.Dak., Ut., Wyo., IDAHO: 6 km E of Bostetler Guard Station, Cassia Co., 26-VII-1985, *Pinus contorta*, M. M. Furniss and J. B. Johnson (5 UI-WFBM, 1 CNC). Adults common in current-year egg galleries in 0.8–2.0-cm-diameter branches on a 30-cm-diameter dead, standing tree with red foliage.

Pityophthorus blandus Blackman

TYPE LOCALITY: Argus Mountains, Calif. BIOLOGY: Unstudied. Polygynous. Specimens collected from 3–8-cm-diameter branches and tree tops (Wood 1982). DISTRIBUTION: USA: Ariz., Calif., Colo., Nev., Ut., IDAHO: City of Rocks, Cassia Co., 25-VII-1985, *Pinus monophylla*, M. M. Furniss and J. B. Johnson (10 UI-WFBM, 4 CNC).

Pityophthorus deletus LeConte

TYPE LOCALITY: Veta Pass, Colo. BIOLOGY: Unstudied. Polygynous. The species is extremely variable and as defined may include more than one species or subspecies (Bright 1981). DISTRIBUTION AND NOTES: MEXICO: Coah., Dgo.; USA: Ariz., Colo., N.M., S.C., Tex., Ut., Wyo., IDAHO: 23 km N of Montpelier, Bear Lake Co., 23-VII-1984, *Pinus flexilis*, M. M. Furniss and J. B. Johnson (1 UI-WFBM). Infesting 0.5–1.0-cm-diameter, shaded-out lower branches. City of Rocks, Cassia Co., 24-VII-1985, *Pinus monophylla*, M. M. Furniss and J. B. Johnson (1 UI-WFBM). Parents, larvae, and teneral adults in 0.4–1.0-cm-diameter twigs with red foliage on live tree. Thirteen km E of Bostetler Guard Station, Cassia Co., 25-VII-1985, *Pinus contorta*, M. M. Furniss and J. B. Johnson (4 UI-WFBM). In long tunnels running lengthwise in 2–3-mm-diameter twigs with red foliage, killed by mistletoe.

Pityophthorus scalptor Blackman

TYPE LOCALITY: Julian, Calif. BIOLOGY: Unstudied. Polygynous. DISTRIBUTION AND NOTES: CANADA: B.C.; USA: Calif., IDAHO: Plummer, Benewah Co., 28-IV-1985, *Pinus ponderosa*, M. M. Furniss (2 UI-WFBM). From a shaded-out branch with red foliage on a small, live tree.

Xyleborinus saxesini (Ratzeburg)

TYPE LOCALITY: Europe. BIOLOGY: The following is based on Schedl (1962) and Batra (1963). The dwarfed males are flightless and apparently mate with their brood sisters, although outcrossing may occur rarely when tunnels intersect (or more commonly when males wander from one tunnel entrance to another [S. L. Wood, personal communication]). Male/female ratios range from 1:7 to 1:39. Females construct a 1-mm-diameter, 3–5-cm-long tunnel radially into stems and large branches of dying or fallen trees. An enlarged cavity (brood chamber) is constructed upward and downward at the end of the tunnel, in which eggs are laid one per niche. Up to 100 eggs are laid per female in groups of 5–12. Larvae feed communally, evidently on the yellowish fungus *Ambrosiella sulfurea* Batra (Batra 1967) which covers the wall of the brood chamber. DISTRIBUTION AND NOTES: EUROPE, ASIA, AUSTRALIA, ARGENTINA, BRAZIL, CHILE; CANADA: B.C., Ont.; USA: Ala., Ariz., Ark., Calif., Conn., Del., Fla., Ga., Ill., Ind., Ia., Kan., Ky., La., Me., Md., Mass., Mich., Miss., Mont., N.H., N.J., N.Y., N.C., Ohio, Ore., Penn., S.C., Tenn., Tex., Ut., Va., Wash., IDAHO: Smith Creek, Boundary Co., 8-VI-1986, *Populus tremuloides*, M. M. Furniss and J. B. Johnson (1 ♀ UI-WFBM). Collected from a larval cradle of a *Trypodendron retusum* (LeConte) gallery in a 20-cm-diameter, fire-scorched, recently fallen aspen.

EXTENSIONS OF KNOWN GEOGRAPHIC OCCURRENCE IN IDAHO

Subfamily Hylesininae

Alniphagus aspericollis (LeConte)

TYPE LOCALITY: Evidently Santa Barbara, Calif. BIOLOGY: Monogynous. Bivoltine (B.C.); damaged or decadent trees are attacked by the respective generation in May and during July to early August. The typical galleries are unbranched and extend about 8 cm (2.0–4.5 cm in Idaho), parallel with the stem. Only stems of about 10-cm diameter and larger are usually infested. Susceptible phloem is usually restricted to a narrow zone in dying trees, between the lower, living stem and the dead distal portion. Several successive generations may infest a stem before it is completely killed (Bordon 1969). DISTRIBUTION AND NOTES: CANADA: B.C., USA: Alas., Wash., Ore., Calif., Ut., IDAHO: Webb, Nez Perce Co., 4-X-1951, W. F. Barr (5 UI-WFBM). Poverty Flat, Krassel Ranger District, Valley Co., 23-IV-1959, *Alnus* sp., M. M. Furniss (3 UI-WFBM). Deary, Latah Co., 1-X-1963, *Alnus* sp., M. M. Furniss (2 UI-WFBM). Falls Ranger Station, Bonner Co., 29-VI-1967, *Alnus* sp., M. M. Furniss (1 UI-WFBM). Orofino, Clearwater Co., 15-III-1983, *Alnus* sp., B. J. Bentz and M. M. Furniss (5 UI-WFBM). Fifty-seven km S of Salmon, Lemhi Co., 19-VII-1985, *Alnus incana*, M. M. Furniss and J. B. Johnson (21 UI-WFBM). Infesting a 12-cm-diameter stem; larvae and pupae present. Two km W of Elba, Cassia Co., 25-VII-1985, *Alnus* sp., M. M. Furniss and J. B. Johnson (4 UI-WFBM). New attacks with only one adult in each; sparse exit holes distally on stem from earlier infestation; larvae (some small) and pupae in older attacks; galleries in this stem were entirely in bark and did not etch the wood. Priest Lake Ranger Station, Bonner Co., 7-VII-1985, *Alnus* sp., M. M. Furniss, J. B. Johnson, and S. J. Gast (4 UI-WFBM). Attacking adults only, including one to two per attack site. Moose Cr., 8 km WNW of Bovill, Latah Co., 21-VIII-1985, *Alnus* sp., M. M. Furniss and S. J. Gast (6 UI-WFBM). Three km N of Pinehurst, Valley Co., 10-III-1986, *Betula occidentalis*, M. M. Furniss (3 ♀, 2 ♂ UI-WFBM). Pairs of beetles in new galleries in green phloem in the base of a 25-cm-diameter, progressively dying tree. First record in other than alder. Spread Creek, 6.5 km N of Hwy 2, Boundary Co., 9-VII-1986, *Alnus* sp., M. M. Furniss and J. B. Johnson (4 UI-WFBM). Taken from base of a 15-cm-diameter dead, leafless alder also containing larvae.

Dendroctonus murrayanae Hopkins

TYPE LOCALITY: Keystone, Wyo. BIOLOGY: Monogynous. Not comprehensively studied. Attacks are restricted to the lower bole near ground; galleries extend 12–20 cm downward to below ground. In Utah, first attacks occurred in the second week of July; eggs were present from 12 July to 9 Sept., laid in groups of 20 to 50 or more. Larvae mine in congress. One and perhaps a partial second generation per year occur in Utah (Wood 1982). DISTRIBUTION AND NOTES: CANADA: Alta., B.C., Man., Ont.; USA: Colo., Mich., Minn., Mont., Ut., Wyo., IDAHO: (The only published record is "Targhee N. F." [Wood 1982], but we have been unable to locate any so-labeled specimens.) Five km SW of Bannock Pass, Lemhi Co., 18–19-VII-1984, *Pinus contorta*, M. M. Furniss and J. B. Johnson (9 ♀, 12 ♂ UI-WFBM). Five *D. murrayanae* galleries, containing 1 dead and 5 live parents, were in the base of a 30-cm-diameter, lightning-struck tree. Two examined galleries had 7 and 23 larvae, probably in their 3rd instar, aligned en masse, side by side in a rather resinous chamber. Associated insects were: *Hylurgops subcostulatus* (Mannerheim) in root crown; and *Ips mexicanus* (Hopkins), *Ips latidens* (LeConte), and *Orthotomicus caelatus* (Eichhoff) in the bole. *Ips mexicanus* was the predominant species throughout the bole above 0.2 m height. Only one *Dendroctonus ponderosae* Hopkins gallery occurred in the tree. A second tree, 10-cm basal diameter, girdled 0.2 m above ground by a porcupine, contained 17 *D. murrayanae* galleries spaced around its circumference. Over 100 live pupae and teneral adults were densely packed in cells in a zone extending from ground level to 5 cm below ground. Three km W of Pass Cr. Summit, Custer Co., 19-VII-1985, *Pinus contorta*, M. M. Furniss and J. B. Johnson (1 ♀, 1 ♂ UI-WFBM). A pair of live beetles was taken from a new gallery in the base of a 23-cm-diameter, 9-m-tall, straw-colored tree. The entrance was 2.5 cm above ground and had external frass similar to that produced by ips beetles; i.e., not resinous (although most *D. murrayanae* entrances have a "pitch tube"). The irregular gallery was not of any characteristic shape, but had two arms, 3 cm and 4 cm long, one running outward, then downward, to the left; and the other outward and upward to the right, with a short side branch. No eggs were present. Wind Lake, Clearwater Co., 17-VII-1986, *Pinus contorta*, M. M. Furniss and E. Christiansen (2 ♂ UI-WFBM). Collected from two current-year galleries 15 cm above ground in a 45-cm-diameter, 22-m-tall, dying tree. Tree crown very sparse, top green, foliage red on lower branches. Bole sparsely infested by *D. ponderosae* in previous year; few brood survived, but blue stain present. Other scolytids present in base were *I. mexicanus* and *Hylurgops* sp.

Comments: We believe that *D. murrayanae* is kept from abundance in its extensively occurring host (in contrast to *D. ponderosae*) by the relative scarcity of trees attractive to it and perhaps by some mechanism, such as a pheromone, that largely excludes *D. murrayanae* from *P. contorta* that are infested with *D. ponderosae*. We collected *D. murrayanae* from 4 trees in Idaho, approximately 10 trees in Montana, and 1 in British Columbia, only 2 of which (mentioned above) had a *D. ponderosae* gallery in them. We know of no proven instance of *D. murrayanae* occurring in a *P. contorta* that was killed by *D. ponderosae*, although millions of that tree species have been killed in the northern Rocky Mountains in the past decade, and *D. ponderosae* has been studied intensively.

Phloeotribus lecontei Schedl

Type locality: La Veta Pass, Colo. Biology: Monogamous. The male constructs an entrance tunnel and the bases of two egg galleries that are then completed by the female. The egg galleries run obliquely across the grain of shaded-out branches in merchantable-sized living trees. Adults and larvae may be present throughout the year; overwintering adults may occur in brood galleries, special hibernation or maturation tunnels, or newly formed parental galleries (Wood 1982). Distribution and notes: CANADA: Alta., B.C.; USA: Ariz., Calif., Colo., Mont., N.M., Ore., Ut., IDAHO: Franklin Co. (Wood 1982). Priest River Experimental Forest, Bonner Co., 28-VI-1967, *Pinus monticola*, M. M. Furniss (1 UI-WFBM). Herd Lake, Custer Co., 3-IX-1978, *Pseudotsuga menziesii*, M. M. Furniss (7 UI-WFBM). Eight km S of Red Ives Ranger Station, Shoshone Co., 16-V-1983, *Picea engelmannii*, M. M. Furniss (1 ♀, 2 ♂ UI-WFBM). All Idaho specimens were collected or reared from shaded-out, 1–2-cm-diameter lower branches of live or freshly killed trees.

Subfamily Scolytinae

Procryphalus mucronatus (LeConte)

Type locality: La Veta Pass, Colo. Biology: Monogynous. Prefers soft, fermenting, dead aspen bark; usually follows primary invasion by *Trypophloeus populi* Hopkins. The gallery is narrower and the bark overlying the gallery is thicker than that of *T. populi* and does not split as it does in the case of *T. populi*. One and one-half to two annual generations (Utah), overwintering as larvae and adults. Eggs appear in late May (Petty 1977). Distribution and notes: CANADA: Alta., B.C.; USA: Alas., Colo., Nev., N.M., Ut., IDAHO: Beaver Canyon, Franklin Basin, Franklin Co. (Wood 1982). Sixteen km E of Wayan, Caribou Co., 22-VII-1984, *Populus tremuloides*, M. M. Furniss and J. B. Johnson

(4 UI-WFBM). Infesting a 30-cm-diameter tree without leaves that apparently died in the previous year. Many new adults and some larvae present only in necrotic areas surrounded by green phloem on trunk within crown, not in branches. Two Mile Canyon Summit, 6.5 km SE of Malad City, Oneida Co., 24-VII-1984, *P. tremuloides*, M. M. Furniss and J. B. Johnson (4 UI-WFBM). A 25-cm-diameter, 7.6-m-tall tree retaining a few dead leaves, with green bark and moist wood, under attack by many *Trypophloeus populi* Hopkins and a few *Trypodendron retusum* (LeConte) on trunk, especially on south aspect. *Procryphalus mucronatus* infesting crotches of branches 1–3 cm diameter, one gallery per crotch. Henrys Lake, Fremont Co., 21-VII-1985, *P. tremuloides*, M. M. Furniss and J. B. Johnson (4 UI-WFBM). Ten km SW of Victor, Teton Co., 22-VII-1985, *P. tremuloides*, M. M. Furniss and J. B. Johnson (2 UI-WFBM). Six km N of Moscow, Latah Co., 22-VIII-1985, *P. tremuloides*, M. M. Furniss (4 UI-WFBM). Spread Cr., 6.5 km N of Hwy 2, Boundary Co., 9-VII-1986, *P. tremuloides*, M. M. Furniss and J. B. Johnson (12 UI-WFBM). Larvae and pupae present in necrotic area surrounded by green phloem in 8–10-cm-diameter portion of stem of tree with dead top and sparse foliage on lower branches. A few new tunnels of *T. retusum* in base.

Trypophloeus populi Hopkins

TYPE LOCALITY: Williams, Ariz. BIOLOGY: The monogamous female excavates an irregular, 2-cm-long gallery just beneath the bark surface of stems or branches of standing, unhealthy, or dying trees. The galleries and larval mines do not show on the inner surface of the bark. One to one and one-half generations per year occur in Utah, overwintering as larvae; eggs are present in July (Petty 1977). DISTRIBUTION AND NOTES: CANADA: Man., N.B., Sask.; USA: Ariz., Colo., Nev., Ut., IDAHO: South Mtn., Owyhee Co., 1-IX-1958, *Populus tremuloides*, M. M. Furniss (10 UI-WFBM). Two Mile Canyon Summit, 6.5 km SE of Malad City, Oneida Co., 24-VII-1984, *P. tremuloides*, M. M. Furniss and J. B. Johnson (4 UI-WFBM); see notes for *Procryphalus mucronatus*, this date. Hwy 31, 10 km SW of Victor, Teton Co., 22-VII-1984, *P. tremuloides*, M. M. Furniss and J. B. Johnson (4 UI-WFBM).

Xyleborus dispar (Fabricius)

TYPE LOCALITY: Germany. BIOLOGY: Infests unthrifty or injured limbs and stems 5-cm diameter and larger. The female tunnels radially into the xylem for 1–3 cm, then constructs two transverse galleries (that may spiral in small branches). The longitudinal galleries may branch in a fashion similar to the original pair (Wood 1982). The female parent carries an ambrosia fungus, *Monilia candida* Hartig, which grows on the wall of her gallery and which is probably a major source of food for her brood (Batra 1963). In British Columbia the beetle has one generation per year, attacking in mid-April. Adults require exposure to cold (overwinter) before emerging in March and April. The sex ratio is 2.2 females per male. The male is dwarfed and incapable of flight. Related species have the capability of reproducing females sexually or males parthenogenetically (Mathers 1940). DISTRIBUTION AND NOTES: EUROPE; CANADA: B.C., N.S., Ont.; USA: D.C., Me., Md., Mass., Mich., N.C., N.J., N.Y., Ohio, Ore., Penn., R.I., Ut., Va., Wash., W.V., IDAHO (listed alphabetically by county): Adams Co.: Council, 4-VI-1982, *Ulmus pumila*, C. Gibson (lost). Benewah Co.: Plummer, 13–28-IV and 7–14-VII-1977, flight trap, M. M. Furniss (2 UI-WFBM); St. Maries (1 UI-WFBM); St. Maries, 31-V-1960, prune (*Prunus* sp.), R. W. Portman (4 UI-WFBM). Boise Co.: Mile High, 11-VI-1974, UV-light, G. A. Shook (2 UI-WFBM). Bonner Co.: Priest River Experimental Forest, 5-VIII-1985, *Alnus* sp., M. M. Furniss, J. B. Johnson, and S. J. Gast (1 ♀ UI-WFBM). Infesting a mostly dead alder stem of 13-cm diameter. Two km E of Nordman, 6-VIII-1985, *Betula paperyfera*, S. J. Gast, M. M. Furniss, and J. B. Johnson (11 ♀, 2 ♂ UI-WFBM). Parents (no brood) attacking 5.0–7.6-cm-diameter portion of stem of a paper birch of 10-cm basal diameter. Foliage discolored, dying. Fall Creek, Boundary Co., 7-VI-1986, *Betula paperyfera*, M. M. Furniss and J. B. Johnson (2 ♀ UI-WFBM). Tunneling in 2.5–6.0-cm-diameter portion of stem of a 15-cm-diameter pushed-over birch. Green leaves sprouting on stem below the dead, infested portion. *Trypodendron betulae* Swaine tunnels abundant in part of stem containing *X. dispar*. Clearwater Co.: Orofino, 17-IV-1952, W. F. Barr (1 UI-WFBM). Orofino, 10-VII-

1977, *Juglans nigra* (4 WSU). Gem Co.: Emmett, 21-VII-1954, cherry (*Prunus* sp.), H. C. Manis (1 UI-WFBM). Kootenai Co.: Coeur d'Alene, 4-VI-1942, prune (*Prunus* sp.), H. E. Shull (4 UI-WFBM). Carlin Bay, Lake Coeur d'Alene, 26-V-1948 (1 UI-WFBM). Deception Creek Experimental Forest, 18-VI to 24-IX-1968, flight trap, M. M. Furniss (1 UI-WFBM). Harrison, 10-V-1969, *Malus* sp., Davis (1 UI-WFBM). Twelve km N of Worley, 7-VIII-1985, *Populus tremuloides*, M. M. Furniss, J. B. Johnson, and S. J. Gast (2 ♀, 2 ♂ UI-WFBM). Infesting lower stem of a dying 25-cm-diameter aspen, also infested with *T. retusum*. Latah Co.: Moscow Mtn., 9-IX-1947, W. F. Barr (1 UI-WFBM). Sixteen km E of Bovill, 16-V-1948, W. F. Barr (1 UI-WFBM). Moscow Mtn., 13-VIII-1970, *Salix scouleriana*, M. M. Furniss (12 UI-WFBM). Nez Perce Co.: Myrtle, 5-VI-1955, W. F. Barr (1 UI-WFBM). Lewiston, 27-IV-1983, *Cornus*, D. White (3 UI-WFBM).

Comments: *Xyleborus dispar* is native to Europe. It was reported in the West (Clarke Co., Wash.) in 1901. The earliest Idaho collection known to us is 1942 (Coeur d'Alene). It infests a wide range of unrelated angiosperms, including fruit trees and ornamentals. It may not yet have reached its eventual distribution in Idaho and may become increasingly important. It merits intensive study.

Xyleborus intrusus Blandford

Type locality: San Geronimo, Guatemala. Biology: Unstudied. Attacks base of recently killed, standing trees in which decay is well underway, at or near ground level (Wood 1982). Male undescribed. Distribution: MEXICO: Chih., D.F., Dgo., Jal., Mex., Mor., Oax., Pue.; GUATEMALA: San Geronimo; HONDURAS: Zamorano; CANADA: B.C.; USA: Ariz., Cal., Col., D.C., Md., Mont., N.C., N.M., Ore., Penn., S.C., S.D., Ut., Va., IDAHO: Stone Airport, Boise River, Ada Co., 1-VIII-1977, ex poplar bark, A. D. Allen (1 A. D. Allen). "Moscow Mts." (Wood 1982). Ten km S of Howe, Butte Co., 18-VIII-1983, *Pseudotsuga menziesii*, J. B. Johnson and F. M. Merickel (656 UI-WFBM). Reared from a rotting stump also occupied by leafcutter bees.

IDAHO SCOLYTIDAE

Hylesininae	Abundance[3]
Hylastini	
Scierus annectens LeConte	U
Scierus pubescens Swaine	R
Hylurgops porosus (LeConte)	C
Hylurgops reticulatus Wood	U
Hylurgops rugipennis pinifex (Fitch)	C
Hylurgops s. subcostulatus (Mannerheim)	C
Hylastes gracilis LeConte	U
Hylastes longicollis Swaine	C
Hylastes macer LeConte	U
Hylastes nigrinus (Mannerheim)	U
Hylastes ruber Swaine	U
Hylastes tenuis Eichhoff	R
Hylesinini	
Hylastinus obscurus (Marsham)	U
Alniphagus aspericollis (LeConte)	U
Tomicini	
Xylechinus montanus Blackman	R
Pseudohylesinus dispar pullatus Blackman	U
Pseudohylesinus granulatus (LeConte)	U
Pseudohylesinus n. nebulosus (LeConte)	C
Pseudohylesinus sericeus (Mannerheim)	R
Dendroctonus brevicomis LeConte	C
Dendroctonus murrayanae Hopkins	R
Dendroctonus ponderosae Hopkins	C
Dendroctonus pseudotsugae Hopkins	C
Dendroctonus rufipennis (Kirby)	C
Dendroctonus valens LeConte	C
Phloeotribini	
Phloeotribus lecontei Schedl	U
Phloeosinini	
Phloeosinus hoferi Blackman	R
Phloeosinus keeni Blackman	U
Phloeosinus punctatus LeConte	C
Phloeosinus scopulorum neomexicanus Blackman	R
Phloeosinus serratus (LeConte)	U
Hypoborini	
Chaetophloeus heterodoxus (Casey)	U
Polygraphini	
Carphoborus carri Swaine	R
Carphoborus pinicolens Wood	R
Carphoborus ponderosae Swaine	R
Carphoborus sansoni Swaine	R
Polygraphus rufipennis (Kirby)	C
Scolytinae	
Scolytini	
Scolytus laricis Blackman	C
Scolytus monticolae Swaine	C
Scolytus multistriatus (Marsham)	U
Scolytus opacus Blackman	C
Scolytus piceae (Swaine)	U
Scolytus praeceps LeConte	R
Scolytus rugulosus (Müller)	C
Scolytus subscaber LeConte	R
Scolytus tsugae Swaine	C
Scolytus unispinosus LeConte	C
Scolytus ventralis LeConte	C
Crypturgini	
Crypturgus borealis Swaine	U

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[3] R = rare (5 or fewer collections), U = uncommon (6–14 collections), C = common (15 or more collections).

Dryocoetini	
Dryocoetes affaber (Mannerheim)	C
Dryocoetes autographus (Ratzeburg)	U
Dryocoetes betulae Hopkins	R
Dryocoetes confusus Swaine	U
Ipini	
Pityogenes carinulatus (LeConte)	C
Pityogenes fossifrons (LeConte)	C
Pityogenes knechteli Swaine	C
Pityokteines elegans Swaine	C
Pityokteines lasiocarpi (Swaine)	U
Pityokteines minutus (Swaine)	R
Pityokteines ornatus (Swaine)	U
Orthotomicus caelatus (Eichhoff)	C
Ips confusus (LeConte)	R
Ips emarginatus (LeConte)	C
Ips integer (Eichhoff)	C
Ips latidens (LeConte)	C
Ips mexicanus (Hopkins)	U
Ips montanus (Eichhoff)	C
Ips pilifrons utahensis Wood	R
Ips pini (Say)	C
Ips p. plastographus (LeConte)	U
Ips tridens engelmanni Swaine	U
Xyloterini	
Trypodendron betulae Swaine	R
Trypodendron lineatum (Olivier)	C
Trypodendron retusum (LeConte)	U
Trypodendron rufitarsis (Kirby)	R
Xyloborini	
Xyleborus dispar (Fabricius)	C
Xyleborus intrusus Blandford	R
Xyleborinus saxeseni (Ratzeburg)	R
Cryphalini	
Trypophloeus populi Hopkins	U
Trypophloeus striatulus (Mannerheim)	R
Procryphalus mucronatus (LeConte)	U
Procryphalus utahensis Hopkins	R
Cryphalus r. ruficollis Hopkins	U
Corthylini	
Conopthorus monophyllae Hopkins	R
Conopthorus ponderosae Hopkins	C
Pityophthorus absonus Blackman	R
Pityophthorus alpinensis G. Hopping	R
Pityophthorus aquilus Blackman	R
Pityophthorus blandus Blackman	R
Pityophthorus boycei Swaine	R
Pityophthorus confertus Swaine	C
Pityophthorus confinis (LeConte)	U
Pityophthorus deletus LeConte	R
Pityophthorus digestus (LeConte)	R
Pityophthorus murrayanae Blackman	R
Pityophthorus nitidulus (Mannerheim)	R
Pityophthorus nitidus Swaine	R
Pityophthorus opaculus LeConte	R
Pityophthorus pseudotsugae Swaine	U
Pityophthorus scalptor Blackman	R
Pityophthorus serratus Swaine	R
Pityophthorus toralis Wood	R
Pityophthorus tuberculatus Eichhoff	U
Gnathotrichus retusus (LeConte)	C
Gnathotrichus sulcatus (LeConte)	R

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LIZARDS AND TURTLES OF WESTERN CHIHUAHUA

Wilmer W. Tanner[1]

ABSTRACT.—This second report on the reptiles of Chihuahua deals with the lizards and turtles of western Chihuahua. Field work was done from 1956 to 1972 and was confined to the area west of Highway 45. General information pertaining to the ecology and geology reported in the section on snakes is not repeated. Ecological and life history information is included in the species accounts where data are available.

In western Chihuahua 16 genera and 49 species and subspecies of lizards and 3 genera and 5 species of turtles are reported. Only one subspecies is described as new (*Sceloporus poinsettii robisoni*), and added data strengthen the diagnosis of others. Three genera (*Sceloporus*, *Cnemidophorus*, and *Eumeces*) contain 28 of the species and subspecies reported.

This is the second article of three on the herpetofauna of the Mexican state of Chihuahua. Article one presented data on the snakes, as well as general information; these will not be repeated. The present report deals with the lizards, a major segment of the reptilian fauna of this state, and briefly with the turtles collected during the various trips. While we at no time concentrated on finding representatives of the order Testudines, we did include them in the collection when found. Therefore, only the scientific name and locality is included in this report.

Perhaps the most complete listing of the lizard and turtle species to date is Smith and Taylor (1950). In their report, 14 genera, 32 species, and 5 additional subspecies of lizards are listed, as are 3 genera and 4 species of turtles. As with the serpents, numerous reports have included lizards and turtles from Chihuahua, but none have been designed to examine as a unit the species occurring in this Mexican state.

Field work was done along Highway 45 from Ciudad Juárez south to the Durango border. No attempt was made to collect east of the highway. Our efforts were, therefore, in areas west of Highway 45, including eight trips into the mountains west of Colonia Juárez and west and southwest of Chihuahua City. We did not enter the Sierra del Nido, an area being investigated by Dr. J. D. Anderson. Collecting was done from May into October 1956–1972. This schedule of trips permitted us to be in Chihuahua during the dry season, May and June, the wet season, from July into early September, and after the heavy summer rains in late September and October. It should be noted that Chihuahua does not have a predictable wet season. Some years the summer rains are spotty, the dry season extending well into July. When the rains do come, there is a major transformation of the entire area. What was apparently a dry, barren hillside soon becomes a green, grassy meadow between the desert shrubs. In the fall, fields of grass, knee- to hip-high, soon develop in the open areas (Fig. 1).

The altitudinal changes, from about 5,000 feet in the desert valleys east of the mountains to the mountains ranging from 7,500 to 9,000 feet, provide a variety of habitats extending west to the Continental Divide. The more gradual ascent from the east is in great contrast to the more sudden descent into the deep canyons and escarpments of the west, particularly in the tributaries of the Río El Fuerte of the southwest. This altitudinal change influences the flora, ranging from desert shrubs in the valleys to the extensive oak and pine forests in the mountains. For the lizards, as was true for the snakes (Tanner 1986), the western highlands have provided for species whose range is restricted to mountains and whose distribution is basically south into Durango rather than north.

During the years (1956–1972) spent in Chihuahua, the habitats (desert valleys, foothills, and western mountains) were being used but not badly abused. Open areas near towns and

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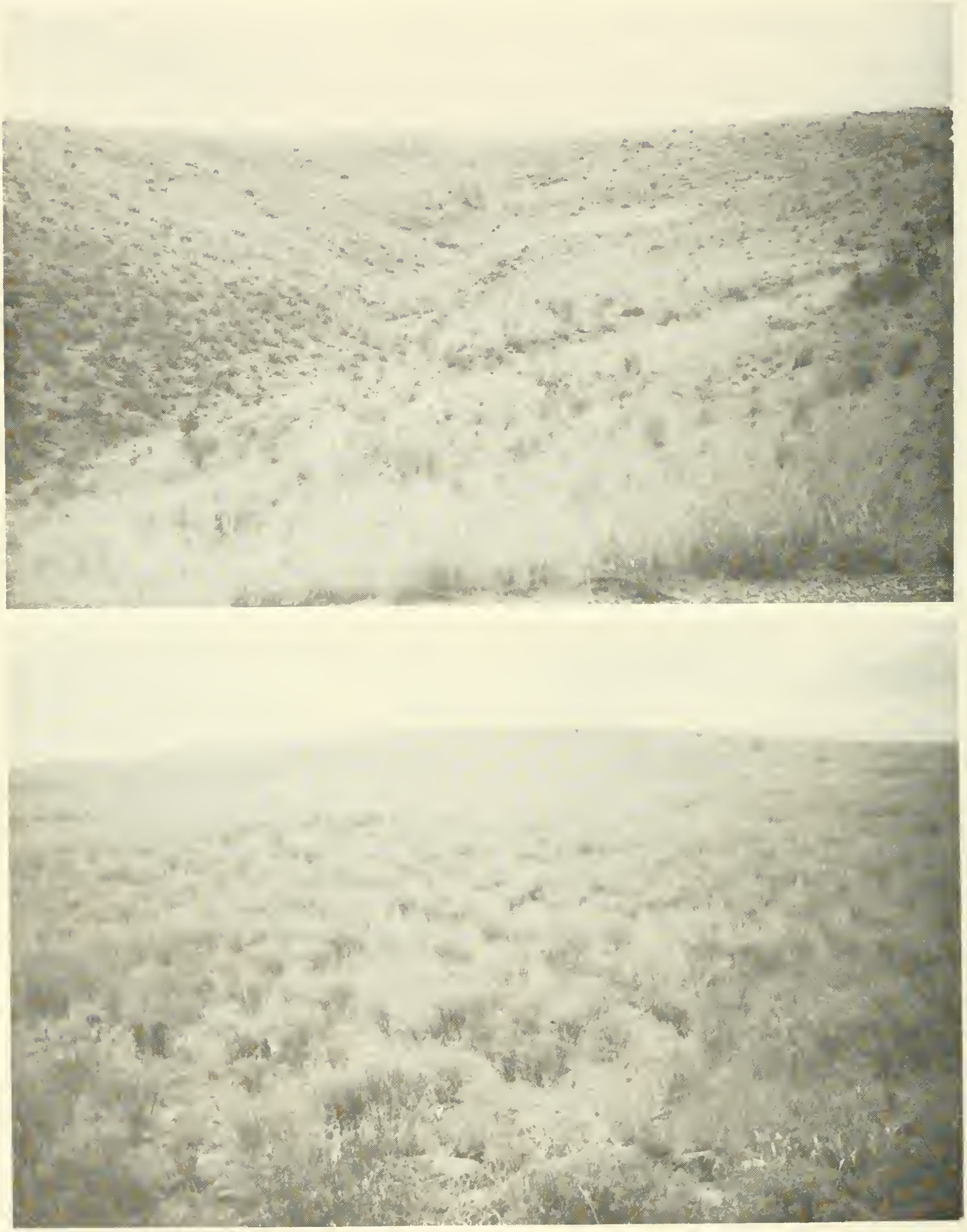

Fig. 1. Views of the area between Casas Grandes and Colonia Juárez: A and B, hills covered with grasses and low-growing shrubs. Photos taken 1 May 1986.

cities were overgrazed, especially during the dry seasons. Bands of apparently unused burros roamed unattended (with the increase of motorized equipment, the burro population has recently been reduced). In the mountains many areas seemed to be pristine except for the removal of large tracts of timber. Except for a few areas of population centered around the mining and timber industries, there were large areas with few inhabitants. Abandoned

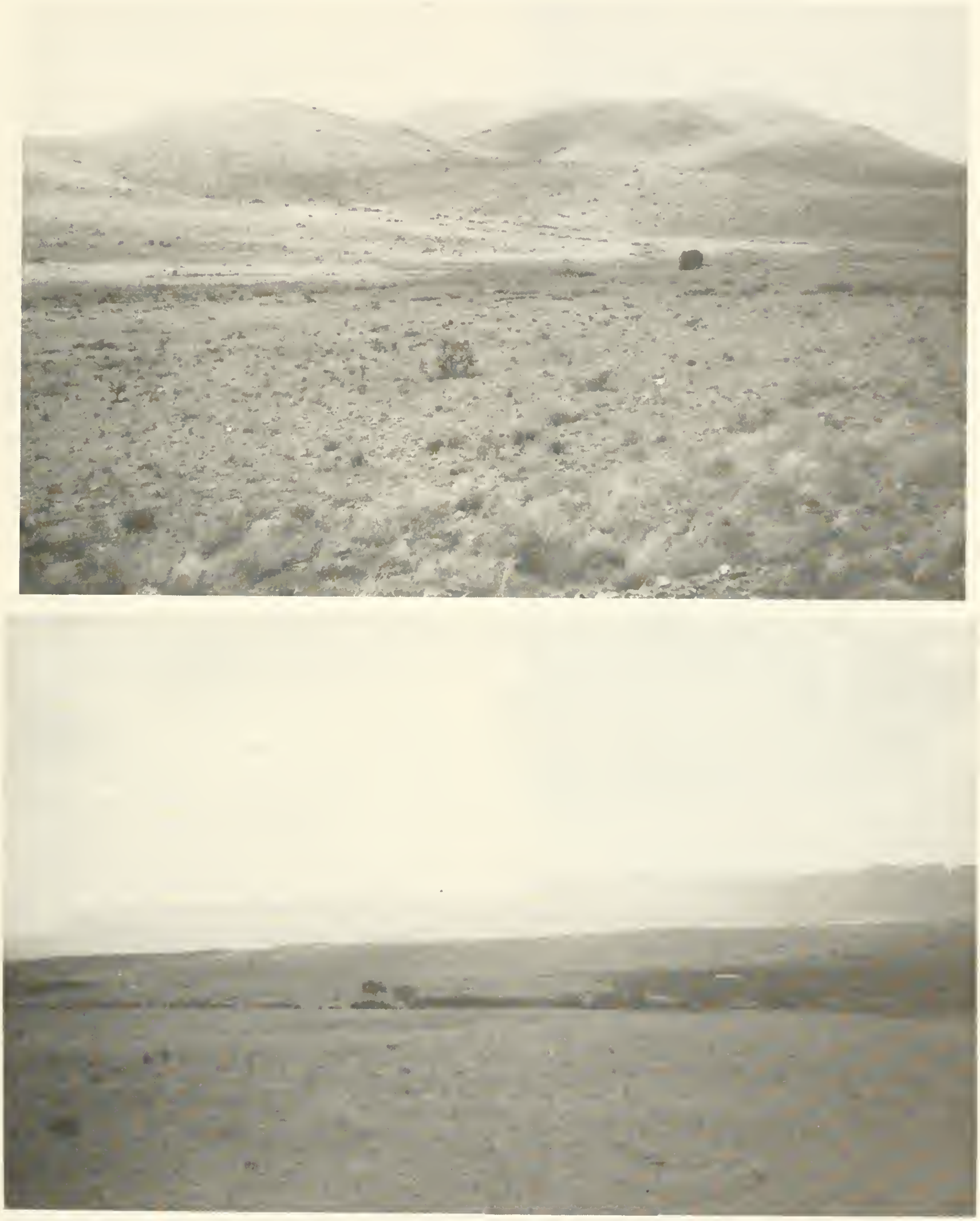

Fig. 1 continued: C, hills covered with grasses and low-growing shrubs; D, view looking southwest across the orchards in the Tinaja Valley and the Sierra Madre Occidental in the distance. Photos taken 1 May 1986.

mines left families stranded and struggling for an existence. In the immediate vicinity surrounding these areas, few suitable collecting sites were found. Thus, our collecting areas were usually removed from the vicinity of towns or cities.

I have been advised that some mountain and streamside areas have in recent years been turned into fields of marijuana and poppies. How safe an American might be collect-

Fig. 2. Mr. and Mrs. Herman Hatch at their home in Colonia Juárez, 30 April 1986.

ing in these areas now is questionable. Nevertheless, our days in the mountains were safe and enjoyable, and at no time did we have any difficulties.

SPECIES ACCOUNTS

The following list includes species collected during our field work, specimens received on loan from other museums, and also literature citations which appear to be valid. Only those references are cited which provide the first descriptions and those considered to be of major importance thereafter. In listing the Testudines, only the localities are indicated to provide the basic distribution for the few widely separated specimens collected. Questionable specimens were identified by Dr. J. E. Iverson. The entire collection has been seen by Dr. J. M. Legler. References dealing more specifically with the kinosternids of Chihuahua are in Conant (1974), Conant and Berry (1978), and Iverson (1981).

Family Kinosternidae

Genus *Kinosternon*

Kinosternon flavescens flavescens Hartweg

Platythyra flavescens Agassiz, 1857a, Contributions to the natural history of the United States 1:430 and 2:01, 5 figs.

Kinosternon flavescens flavescens: Hartweg, 1938, Occ. Papers Mus. Zool. Univ. of Michigan 371:1–5; Iverson, 1979, Copeia (2):212–225.

Approximately 2 mi S of Las Palomas (at a big spring), 1 (BYU 14650).

80 mi S Ciudad Juárez (on Hwy. 45), 1 (BYU 21721).

65.9 mi N Ciudad Chihuahua, 1(BYU 22619).

Kinosternon sonoriensis LeConte

Kinosternon sonoriensis LeConte, 1854, Proc. Acad. Nat. Sci. Philadelphia 7:180–190; Iverson 1981, Tulane Studies in Zoology and Botany, 23 (17:7–74).

Cerocahui, 4 (BYU 14625–28).

Río Bavispe, below Tres Ríos, 1 (BYU 14629).

REMARKS.—Iverson (1981) questioned the occurrence of this species in the Río Fuerte basin. Yet four specimens were taken from a small creek at Cerocahui. This creek drains into the Río Oteros, the northern tributary of the Río Fuerte. Recently, Dr. Iverson reexamined two specimens of the series and confirmed their identity.

The Río Oteros has its headwaters in the same general area as the Río Tomochic, a tributary of the Río Papigochic which is a tributary of the Río Yaqui. The nearness of these streams to each other suggests that the movement from one drainage system to the other is likely, or perhaps stream piracy may have facilitated the southward distribution.

Kinosternon hirtipes murrayi Glass & Hartweg

Kinosternon murrayi Glass & Hartweg, 1951, Copeia 1951:50–52.

Kinosternon hirtipes murrayi Schmidt, 1953, A checklist of North American amphibians and reptiles, p. 89; Iverson, 1981, Tulane Studies in Zoology and Botany 23(1)1–74.

Approximately 2 mi N Casas Grandes 5 (BYU 14132–5 and 15457).

Río Santa María near Galeana, 3 (BYU 16846–8).

Río Santa María above bridge west of Galeana 10 (BYU 15266–75).

Genus *Chrysemys*

Chrysemys picta bellii (Gray)

Emys bellii Gray, 1831, Synopsis reptilium, p. 31.
Chrysemys picta bellii: Bishop and Schmidt, 1931, Publ. Field Mus. Nat. Hist., Zool. Ser. 18:136.
Río Santa María, above bridge west of Galeana, 3 (BYU 15263–4, 15267).

Genus *Terrapene*

Terrapene ornata luteola Smith & Ramsey

Cistudo ornata Agassiz, 1857b, Contributions to the natural history of the United States 1:445.
Terrapene ornata luteola: Smith and Ramsey, 1952, Wasmann J. Bio. 10(1):45–54.
2 mi E Colonia Dublán, 2 (BYU 14646–7).
West edge of Colonia Dublán, 3 (BYU 15449–51).

Family Gekkonidae

Genus *Coleonyx*

Coleonyx brevis Stejneger

Coleonyx brevis Stejneger, 1893, North American Fauna no. 7:163–64; Chrapliwy and Fugler, 1955, Herpetologica 13:121–128.
2 mi N 6 mi E Camargo 1 (KU 33874).

Smith and Taylor (1950) list *C. brevis* from southern Texas southward through eastern Chihuahua. We saw no specimens in central or western Chihuahua. The distribution map provided by Klauber (1945) places the genus *Coleonyx* barely in the eastern edge of Chihuahua. The specimen from NE of Camargo and records from Coahuila (Chrapliwy and Fugler 1955) suggest that this species may be present in much of eastern Chihuahua.

Whether *C. v. bogerti* extends into Chihuahua from southeastern Arizona and southwestern New Mexico must be demonstrated, even though the terrain is seemingly similar in northwestern Chihuahua. Dixon (1970) does not extend the range into Chihuahua.

Genus *Phyllodactylus*

Phyllodactylus tuberculosus saxatilis Dixon

Phyllodactylus tuberculosus saxatilis Dixon, 1964, New Mexico State Univ. Bull. 64(1):31–36.
Urique, 1 (KU 56210).

Cope (1898–1900) lists a specimen collected at Chihuahua City by E. Wilkinson, and Dixon (1964a), a specimen for Batopilas. I have seen only one specimen from Chihuahua and recognize the similar habitat in southwestern Chihuahua and adjoining Sinaloa. It is not to be expected in central and eastern Chihuahua, certainly not at Chihuahua City. The distribution of this species is indicated by Dixon (1964a:124, map 2) and does not include any area east of the Continental Divide.

Family Iguanidae

Genus *Anolis*

Anolis nebulosus (Wiegmann)

Dactyloa nebulosa Wiegmann, 1834, Herpetologica Mexicana, p. 47.
Anolis nebulosus Bocourt, 1873, Mission Scientifique au Mexique, 2:68–69.
Anolis nebulosus Fitch, 1978, Milwaukee Public Mus. Contr. Biol. and Geol., Bull. 20:1–15.
6–7 mi W below La Bufa road bridge across Río Urique, 6 (BYU 22691–7).
Urique, 3 (BYU 14335–7).
2 mi N Maguarichic, 1 (BYU 16915).

There is some variation among the specimens available. However, with some hesitation, I have designated them as *nebulosus*, recognizing that Smith and Taylor (1950) listed *nebuloides* for the species occurring in Chihuahua. It seems more logical to relate the specimens from southwestern Chihuahua to those populations in adjoining Sinaloa and Sonora. This was also the conclusion reached by Duellman (1961) and Hardy and McDiarmid (1969). The habitat in the valley and tributaries of the Río El Fuerte are extensions from the coastal plain, providing a continuum of environment that does not seem to allow for two similar species.

The characters such as keeled ventrals, which are equal to or only slightly larger than the mid-dorsals, the interparietal larger than ear opening, and the faint yellowish pink on the gulars suggest the above designation for the anoles in southwestern Chihuahua.

Genus *Ctenosaura*

Ctenosaura hemilopha macrolopha Smith

Cyclura (Ctenosaura) hemilopha Cope, 1863, Proc. Acad. Nat. Sci. Philadelphia, pp. 105–106.
Ctenosaura hemilopha macrolopha Smith, 1972, Great Basin Nat. 32(2):104–111.
El Realito, at Tarahumara dwelling, 1 (BYU 22675).
Urique, 9 (BYU 14616–24).

Smith (1972) described and listed the distribution of this subspecies as occurring in the coastal plain of northern Sinaloa, southern Sonora, and with narrow projections extending eastward into the deep river valleys of western Chihuahua. The area of distribution occurs primarily in the low shrub and thorn forests at elevations extending from the Gulf Coast eastward to elevations of 2,000–2,500 feet. Its distribution in Chihuahua is only in the deep barrancas where the coastal habitat has been extended eastward along the rivers.

Genus *Holbrookia*

Holbrookia maculata approximans Baird

Holbrookia approximans Baird, 1858, Proc. Acad. Nat. Sci. Philadelphia, 1858:253.

Holbrookia maculata approximans Stejneger, 1890a, North Amer. Fauna, no. 3.

Montezuma Mountain (between Casas Grandes and Colonia Juárez), 4 (BYU 11370, 15752, and 17098–9).
4 mi E Nuevo Casas Grandes, 3 (BYU 14123–5).
Northwest Chihuahua (NW corner of state), 1 (BYU 30642).
Approximately 18 mi from Colonia Juárez up Tinaja Canyon, 4 (BYU 14415–6, 15790 and 39998).
6.5 mi N Chihuahua City, 1 (BYU 15310).
26 mi S Ascensión, 6 (BYU 15782–5 and 15788–9).
N of Blue Mts. near Garcilancito Saw Mill, 1 (BYU 13597).
Río Bavispe below Tres Ríos, 5 (BYU 13448, 13450, 13452, 13454, and 13469).
Cerocahui, 2 (BYU 14386 and 14606).
8 mi N Cerocahui, 3 (BYU 15674–6).
7 mi S Cuiteco, 2 (BYU 15693–4).
11 mi SW Cuiteco, 2 (BYU 15777–8).
El Kilo, 1 (BYU 14339).
30 mi S Ciudad Juárez, 1 (BYU 15209).

The Chihuahua series represents samples from a wide area of central, northern, and western parts of the state. Within this area the following scale and color patterns were obtained: Ventrals 60–80 (69.8), 61–75 (67.65); femoral pores, totals, 18–25 (22.75), 14–27 (21.50). Adults range in S-V length from 50 to 66.5 mm. The greatest total length is 116 mm. Adult males were larger than females in both S-V and total length. In males the tail was always longer than the S-V length, ranging from 52 to 57 percent. In females the ratio is 40–48 percent.

Five females were gravid and contained 3–7 yolking eggs. One of the five females (13454) taken along the Río Bavispe on 29 May 1956 contained 5 eggs. The eggs were round and approximately 3.5 mm in diameter. In July and August the eggs were much larger (14606, 8.5, and 14125, 9.5 mm). The smallest gravid female was 46 mm S-V and the largest 60 mm.

Dorsal color patterns were variable, ranging from those with two rows of chevron spots from nape to tail to those from east of Nuevo Casas Grandes that are almost uniformly plain gray. In the latter the diagonal black bars on each side of the abdomen are faint in contrast to others. In females the diagonal bars tend to be faint in contrast to the males and do not have the blue edging common in adult males. The dorsal pattern in males, the two rows of chevron spots, may resemble that of females, but the ground color is usually a darker gray. In one specimen (BYU 17098) from west of Casas Grandes, an adult male, the dorsum on each side of a plain dark gray median area is speckled with small white spots, each spot involving 1–3 scales. The dark chevron spots usually present are absent anteriorly but present posteriorly and on the base of the tail.

The female specimen from 30 mi S of Ciudad Juárez was taken in a sand dune area and should perhaps represent the subspecies *bunkeri*. The dorsal pattern is light gray to almost cream color, without spots except near the tail. Its basic color and diagonal belly spots are similar to three specimens from 4 mi E of Nuevo Casas Grandes, that is, faint and without any surrounding blue. Other scale characters are: ventrals 75 and femoral pores 11–11. Total length 116, S-V 56.5, hind leg approximately 42 mm. Percent of tail to S-V length 51.5, which is higher than in females from the central valleys; ratio of hind leg to snout-vent length, 0.75. The head scales are not noticeably different from *H. m. approximans;* that is, the supralabials are not flared and appear the same as others in this series.

Because I cannot recognize differentiating characters between this specimen and most others in the series, I have retained it in this subspecies. A larger series from this sand dune area, which is near the type locality, may prove the existence of the subspecies *bunkeri* in northeastern Chihuahua (Smith 1935).

Genus *Cophosaurus*

Cophosaurus texanus scitulus Peters

Cophosaurus texanus Troschel, 1850 (1852), Wiegmann's Arch. für Naturg., Jahrg. 16, 1:289.

Holbrookia texana: Baird and Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia 6:124.

Holbrookia texana scitula Peters, 1951, Occa. Pap. Mus. Zool., Univ. Michigan 537:8–11.
3 mi S Las Palomas, 1 (BYU 14507).
6 mi N Chihuahua City, 5 (BYU 15301, 15304, 15311, 15333, and 16985).
19 and 33 mi S Chihuahua City, 2 (BYU 15712 and 15814).
16 mi S Ascensión, 2 (BYU 17015–16).

The ventrals range from 75 to 95 (82.2) and the femoral pores are 11–16 (14.1), total 25–31 (28.2). Other scale and color patterns are well within the parameters set forth in the original description. Three male specimens from northern Chihuahua north of Highway 10 (El Sueco–Colonia Juárez) have more ventrals, 84–95 (90.0), than those from near Chihuahua City and south, 75–83 (78.3). Peters (1951) examined 19 specimens, 8 from the north and 11 from south Chihuahua, but did not note such a variation. The type from 16 miles north of Tucson, Arizona, is a male with 83 ventrals, which is approximately average for males reported for Arizona (Peters 1951:16).

In Chihuahua, this species seemed to be gregarious and to inhabit rocky outcroppings. None was found in the brushy valleys unless a rocky bank occurred along a stream bed or an arroyo.

The series ranged in S-V size from 26.2 to 81.0 mm. Four hatchlings were collected. The smallest, 26.2 mm, was found 23 July 1958, 19 miles south of Chihuahua City near Highway 45. Three were taken 9 September 1959, 6 miles north of Chihuahua City, and measured 28.8, 31.2, and 34 mm.

Genus *Crotaphytus*

Crotaphytus collaris fuscus Ingram & Tanner

Crotaphytus collaris fuscus Ingram and Tanner, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 13(2): 1–29.
6.5 mi N and 1.5 mi W Chihuahua City, 26 (BYU 14211–12, 15305, 15325–31, 15817–22, 16969–77, 17810).
Colonia Juárez, 1 (BYU 13736).
28.6 mi S Las Palomas, 1 (BYU 17014).
12 mi SE Nuevo Casas Grandes, 1 (BYU 15184).
Tinaja Canyon NW Colonia Juárez, 4 (BYU 15185–8).
5 mi W Ricardo Flores Magón, 5 (BYU 13382–6).
18.5 mi E Ricardo Flores Magón, 2 (BYU 13410–11).

Ingram and Tanner (1971) described the subspecies *fuscus* from the series listed above and compared the types to a large series from the Great Plains, New Mexico, Arizona, Utah, and Coahuila. From these data it was determined that *fuscus* was unique, having a dull color pattern when compared to other subspecies in the *collaris* complex. The predominant greens and yellows were not present, with only browns and black involved in the throat, nape, and collar patterns. Furthermore, the basic ground color is white or light cream, both dorsal and ventral. This is in contrast to the green body of *collaris*, *baileyi*, and *auriceps* and the infusion of yellow to gold coloring on legs, body, and particularly the head of *auriceps*.

The nape collars are widely separated dorsally with the first having 10 or more scales between the two lateral dark bars and with usually 5 dorsal scales separating the second collar. The ventral ends of the second collar extend onto the forearm.

The distribution extends south through central Chihuahua from southern New Mexico and southeastern Arizona, and west into north central Sonora, where intergradation occurs with *baileyi* and perhaps also with *dickersonae*. *Crotaphytus c. nebrius* Axtell & Montanucci (1977) appears to be an intergrade between *fuscus* and *baileyi*. The extent of the distribution of *fuscus*, *dickersonae*, and *baileyi* in northern and central Sonora and the extent of the distribution of *fuscus* in Chihuahua are not yet fully determined.

Crotaphytus (Gambelia) wislizenii wislizenii Baird & Girard

Crotaphytus wislizenii Baird and Girard, 1852b, Proc. Acad. Nat. Sci. Philadelphia (type locality near Santa Fe, New Mexico). In Stansbury's explorations and survey of the valley of the Great Salt Lake of Utah, pp. 340–341, pl. 3.
Gambelia wislizenii wislizenii Smith, 1946, Handbook of lizards, pp. 159–164, pl. 30.
Crotaphytus wislizenii wislizenii Schmidt: 1953, A check list of North American amphibians and reptiles. Amer. Soc. Ichy. and Herpt., p. 117.
1 mi S Ahumada, 3 (USNM 104738–40).
6 mi SW Rancho María, 1 (USNM 10471).
Rancho María, near Progreso, 10 (USNM 104741–50).
Santa María, 1 (CHNH 1639).
Lake Santa María, 1 (USNM 47414).

This species apparently occurs only in northern Chihuahua between Ciudad Juárez and Moctezuma (Smith and Taylor 1950 list two localities, 11 mi S Ahumada and 2 mi S

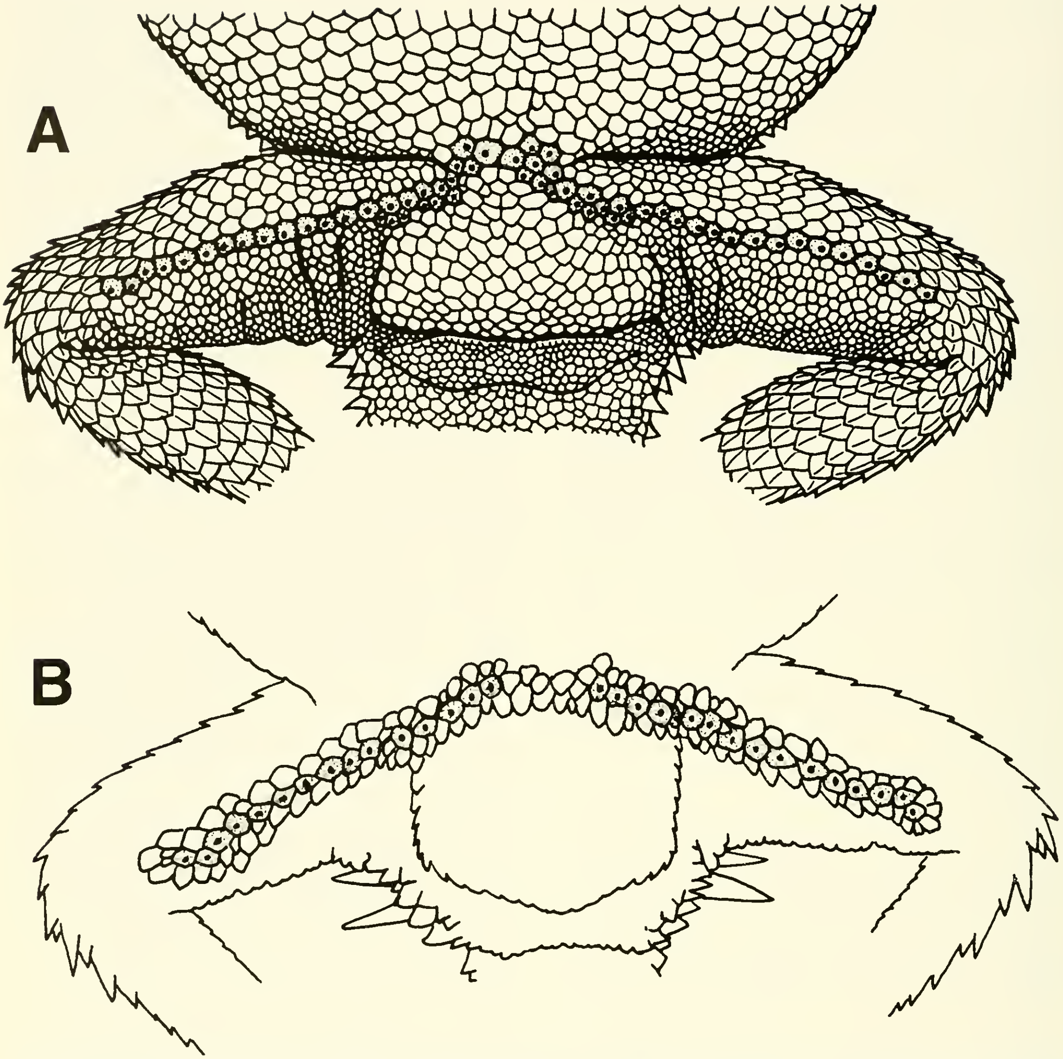

Fig. 3. Variations in the femoral pores of A, *Phrynosoma o. bradti* (BYU 14314) and B, *Phrynosoma o. orbiculare* (BYU 41295).

Moctezuma). We spent only a few hours collecting in these localities and did not see a leopard lizard. In areas where we spent considerable time south and west of El Sueco, none were seen. The mostly brushy habitat is more suited to this species than are the sandy desert valleys in northern Chihuahua.

Genus *Phrynosoma*

Four species of horned lizards are known to occur in Chihuahua. Two are widespread in the desert valleys east of the Sierra Madre (*cornutum* and *modestum*), and the third (*douglassii*) occurs along the eastern foothills and westward in the northern mountains. The distribution of *orbiculare* is least understood. Its locality records indicate a distribution in the mountains of southern Chihuahua. Taylor and Knobloch (1940) list two specimens from or near Mojarachic and report the femoral and preanal pores to be 24–24 and 25–26, with each femoral series meeting medially or only narrowly separated. Reeve (1952) apparently examined these specimens but failed to point out this unusual increase in pores, indicating only that in *orbiculare* the pores number 14–15 and are separated medially by five preanal scales. Horowitz (1955) reviewed the species *orbiculare* and described as new the Durango and Chihuahua populations.

Phrynosoma orbiculare bradti Horowitz

Lacerta orbicularis Linnaeus, 1789, Systema Naturae, ed. 12, Vol. 1, p. 1062 (part based on Hernández).
Phrynosoma o. orbiculare Smith, 1934, Trans. Kansas Acad. Sci. 37:200.
Phrynosoma o. bradti Horowitz, 1955, Amer. Midl. Nat. 54(1):204–218.
West rim, Barranca del Cobre, west of Urique, 1 (BYU 14314).
Cienega la Prieta (north of Tubares on mountain well above the Río San Miguel), 1 (BYU 22659).
21 mi S Miñaca, 1 (ANSP 20001).
6 mi S and 5 mi E San Juanito, 1 (KU 44163).
15 mi S and 6 mi E Creel, 1 (KU 44164).
7 mi SE Cerocahui, 1 (KU 56211).
1 mi NW Urique, on Río Urique summit of Punto Gallego, 1 (NMMZ 41952).

The specimens listed above were not included in the original description. The Chihuahua series now available in museum collections consists of at least 15 specimens. Additionally, I examined one of those seen by Horowitz (1955), ANSP 20001. Perhaps the most significant character in this series is the large number of femoral pores. Those examined by me range from 44 to 70 and average 53.2. This is an increase over those reported in the original description (43–55, $\bar{x} = 49.0$). A character of importance is the development of two or three rows of pores in 6 of 7 specimens examined (Fig. 3). The second or third rows are shorter, ranging from 5 to 8 pores on a thigh, and they may or may not meet at the ventral midline. This increase in rows may account, in part at least, for the large number of pores. A single row on each femur, not meeting medially, has apparently resulted in fewer pores in the populations south of Chihuahua; however, this was not discussed by Horowitz (1955).

The following scale patterns were observed: ventrals from gular fold to femoral pores 43–53 (46), and 10–14 from femoral pores to anus; supralabials 8–10; infralabials 6–9; scales in lateral fringe variable, 21–29. Color pattern with less pigmentation, both dorsal and ventral surfaces; 3 or 4 narrow brown cross bars on dorsum of body and venter with small spots or light reticulations. A specimen of *P. o. orbiculare* (BYU 41295) from 4 mi N Trés Cumbres, Distrito Federal, is heavily pigmented both dorsally and ventrally, with 7 dark cross bars edged posteriorly by a cream bar, pores 15 on each thigh and separated by 5 scales.

It is not the intent here to further examine the subspecies occurring south of Chihuahua. However, an in-depth examination of the color and scale patterns would, I believe, provide additional diagnostic characters not provided in the study by Horowitz (1955). The scale patterns between the occipital spines and anterior to the parietal show noticeable variations between the subspecies *bradti* and *orbiculare*. The distribution of *bradti* is poorly known for southern Chihuahua and northern Durango. Horowitz indicates that the range may extend into Sonora and, if so, then perhaps into the general area of the mountains near Yecora.

Montanucci (1979 and 1981) adds considerably to an understanding of the systematics, distribution, and ecology of *P. orbiculare*. The subspecies *bradti* is retained to include *durangoensis*. His expanded report on the habitats and food habits is essentially what we observed for *Phrynosoma* in the foothills and mountains of western Chihuahua.

Phrynosoma cornutum Harlan

Agama cornuta Harlan, 1825, J. Acad. Nat. Sci. Philadelphia 4:299.
Phrynosoma cornutum Gray, 1831, Syn. Rept. in Griffith's Anim. King., p. 45.
20 mi S Las Palomas, 2 (BYU 16967–8).
45 mi S Ciudad Juárez, 1 (BYU 21716).
5 mi W Ricardo Flores Magón, (BYU 13388).
14 mi W Ricardo Flores Magón, 1 (BYU 15335).
19 mi W Ricardo Flores Magón, 3 (BYU 13414–5 and 13401).
1 mi W Sueco, 1 (BYU 15361).
3 mi E Buenaventura, 1 (BYU 40078).
5 mi E Colonia Dublán, 2 (BYU 14126, 14649).
3.8 mi SE Nuevo Casas Grandes, 1 (BYU 15585).
7 mi NW Chihuahua City, 1 (BYU 15824).
37 mi S Chihuahua City (on Road 45), 1 (BYU 32032).

Reeve (1952) added the following additional localities: Ascensión (27 mi N), Casas Grandes, 19 mi E Casas Grandes, 14 mi E Casas Grandes, Chihuahua City, Moctezuma, 30 mi N Moctezuma, Río Santa María near Progreso, 12 mi E San Buenaventura, Santa María, Santa Rosa, and White Water Monument. These and other records are referred to by Reeve and include collections reported from the Field Natural History Museum (Schmidt and Owens 1944) and from the U.S. National Museum (Reeve 1952).

The distribution of this species, as indicated by the above records, is in the desert flats east of the foothills of the Sierra Madre Occidental. Their habitat is primarily in the low shrub desert flats and along the edges of the rocky foothills that extend as low ranges east of the western mountains.

Phrynosoma cornutum appears to be the most common horned lizard seen in the low valleys of central and eastern Chihuahua. However, *P. modestum* may be as abundant in this habitat, but its smaller size and camouflaged pattern render it less obvious.

Phrynosoma modestum Girard

Phrynosoma modestum Girard, 1852, Stansbury's explorations and survey of the valley of the Great Salt Lake, pp. 361–365, pl. 6; Smith and Taylor, 1950, Univ. Kansas Sci. Bull. 33(2):313–380. (Type locality of this species restricted to Las Cruces, New Mexico, p. 359).

9 mi E Nuevo Casas Grandes, 2 (BYU 13841–2).
1 mi W Sueco, 1 (BYU 15362).
20 mi S Las Palomas, 1 (BYU 14607).
Colonia Juárez, 1 (BYU 17043).
6.7 mi N Chihuahua City, 6 (BYU 15306, 16980–16984).
33 mi S Chihuahua City (on Highway 45), 1 (BYU 15813).

Reeve (1952) listed 11 specimens from the following localities: 1 mi S Villa Ahumada, Chihuahua City, 4 mi NW near Progreso Río Santa María, Santa María, and 8 mi N Samalayuca.

The distribution in Chihuahua is in the low desert valleys of the north, extending south and east of the mountains to northeastern Durango and eastern Coahuila.

The tympanum is concealed in a fold between the angle of the mouth and the last large temporal spine. Unlike other species in the genus, in most Chihuahua specimens there is no visible tympanic membrane. When a membrane is present, it is small and deeply concealed in a temporal fold of skin.

In the series (12 specimens) from Chihuahua the femoral pores range from 9 to 13 and average 10.3 on each femur. In a series from southern Arizona, New Mexico, and Texas, the pores range from 9 to 16 and average 12.0. Smith (1946) lists the femoral pores as 10–15 for the species, and Reeve (1952) lists them as 7–13. The high counts (11–16) came from five specimens from Graham County, Arizona, with only 3 of the 10 femoral pore counts being less than 14.

The color pattern of this species rendered it difficult to see unless an individual moved. On 21 July 1960, on the gradual slopes of the bajada extending west from Highway 45, a few miles north of Chihuahua City, we collected five, none of which were seen until disturbed by our walking close to them. Their escape from predators undoubtedly depends to a great extent on the ability to blend their body color pattern to match closely the substrate of their habitat.

Phrynosoma douglassii (Bell)

Phrynosoma douglassii occurs in both the foothills of central Chihuahua and in the highlands north of the Río Papigochic. Those along the eastern edge of the mountains from Colonia Juárez to at least the area near Cuauhtémoc and including the population reported by Van Devender and Lowe (1977) belong to the subspecies *hernandesi*. Those taken in the mountains southwest of Casas Grandes have the basic characteristics of *brachycercum*.

Since the distribution of the subspecies of *douglassi* in Chihuahua and Durango is poorly known, one can only speculate as to the extent of the area occupied by each subspecies. Furthermore, the type locality of *brachycercum* may be as Reeve (1952) listed, 5 miles north of Durango City, or it may be in the mountains to the west. A specimen (BYU 41328) taken 29 September 1974 at El Salto suggests that *brachycercum* also occurs in the mountains of Durango. We are not suggesting that this subspecies does not occur in the foothills north or west of Durango City but rather that its distribution may occur over a wide area in the south and extend north only in the higher mountains. We need considerably more specimens before the distribution of this species and its subspecies will be understood.

I have not seen the specimens from the vicinity of Santa Bárbara, Chihuahua, reported by Reeve (1952). The area west of the city rises abruptly to 8,000–9,000 feet and may represent the habitat from which the specimens came. In spite of these speculations we will, with this report, have more information than has been available to date.

Phrynosoma douglassi hernandesi Girard

Tapaya hernandesi Girard, 1858, United States exploring expedition for the years 1838, 1839, 1840, 1841, and 1842 under the command of Charles Wilker ASN; Vol 20:395, herpetology.

Phrynosoma douglassi hernandesi Cope, 1898 (1900), Report U.S. Nat. Mus., p. 413, fig. 70.
Colonia Juárez (environs), 15 (BYU 13508, 14333, 15193–15202, 15750, 16966, and 17110).
13 mi E Cuauhtémoc, 3 (BYU 14484, 15203, and 15691).
Sierra del Nido, 2 (UTEP 2520–1).

Van Devender and Lowe (1977) list 26 specimens from the following localities: General Trías, 25 km N Gómez Farías on Mexico 10, Temosachic, and Yepomera.

These specimens are placed in this subspecies on the basis of the following characteristics: tail longer than width of head at the temporals and chest scales smooth without keels on any scales. In males the tail is noticeably longer than in females, giving a greater difference when compared to head width. Although all females have longer tails than their head width, in some it is only by 1–5 mm.

Large specimens (133 mm or more in total length) taken in late June or July were brightly colored with red and pink markings around the mouth and on the sides. The dorsal body blotches were distinct when an individual was in hand. On the ground the pattern blended with the substrate so that few were seen before they moved.

Phrynosoma douglassi brachycercum Smith

Phrynosoma douglassi brachycercum Smith, 1942, Proc. U.S. Nat. Mus. 92(3153):362–3; Reeve, 1952, Univ. Kansas Sci. Bull. 34, part 11, no. 14; pp. 916–918.
Chuhuichupa, 2 (BYU 14502–3).

Both specimens are females with the head width and tail length equal and with some of the chest scales with keels. Both are adults 116–117 mm in total length, of which only 25–26 mm is tail. In one, the head width at the temporals is 25 mm, and in the other 26.

The Chuhuichupa Valley lies in the headwaters of the Río Bavispe. The town is nearly surrounded by grassland and meadows with pine forests on the east, south, and west. Apparently the grass areas and meadows north of the town had been present for a long time and were not the result of timber removal. It was in this area that the lizards were found. This valley is similar to some of the high mountain and plateau basins of southern and central Utah where *P. d. hernandesi* occurs.

Genus *Sceloporus*

The genus *Sceloporus* is the most widespread and diversified lizard genus in Chihuahua. It is represented by nine species, two of which are represented by two or more subspecies. This is based only on collections made west of Highway 45. Additional species, such as *S. merriami*, may enter along its eastern border from populations in Coahuila (Smith and Taylor 1950:132). Few habitats have not been occupied by at least one member of the genus; representatives are found in the deserts, along wooded streams, and in the various mountain habitats.

Few North American saurian genera have undergone such pronounced speciation as has *Sceloporus*. Smith (1939) and Larsen and Tanner (1974, 1975) have attempted to determine relationships within its members by arranging them in related groups. By using 80 characters and applying numerical statistical methods to them, Larsen and Tanner (1974, 1975) concluded that there were three distinct species groups in the genus *Sceloporus*. Furthermore, it was concluded that the most primitive group, including such species as *gadoviae*, *couchi*, and *merriami*, had basic characters which set them apart from the other two groups and thus should be placed in a separate genus, *Lysoptychus* Cope (1888).

With *merriami* occurring in eastern Chihuahua, there are representative species of all three groups, as designated by Larsen and Tanner (1975), occurring in Chihuahua. The speciation, resulting in 60 or more species, is a further indication of the genetic flexibility of this genus, as now recognized, which has established itself abundantly and prominently in nearly all, if not all, habitat niches. Such species as *jarrovii* and *poinsettii* were apparently present (one or both) at nearly all collecting sites. A species of this genus was generally one of the first to be collected.

Our field trips have traversed much of the state except the mountains of southern Chihuahua and the eastern deserts. The collections resulting from these trips will serve as the basic material used in the following species reports. Only when it is deemed necessary for clarity is outside material included.

Sceloporus clarkii clarkii Baird & Girard

Sceloporus clarkii Baird and Girard, 1852a, Proc. Acad. Nat. Sci. Philadelphia 6:127.
Sceloporus clarkii clarkii Cope, 1875a, U.S. Nat. Mus. Bull. 1:49–92.
Río Bavispe, below Tres Ríos, near Chihuahua-Sonora line, 24 (BYU 13369–70, 13429, 13431–33,

13494–13502, 13506, 13584–89, 13592, and 14554).
2 mi W Colonia Juárez, 2 (BYU 13440–1).
Red Rock, 12 mi up Tinaja Canyon from Highway 10, 1 (BYU 13854).

Sceloporus clarkii clarkii was found in the canyons of northern Chihuahua on both sides of the Continental Divide. Specimens were not found in the highlands but at intermediate areas where cottonwoods and other trees occurred along streams. We did not collect this subspecies south of Colonia Juárez. Van Devender and Lowe (1977) did not report it from Yepomera, and I have no report of its occurrence from other studies south of those reported above.

The scale patterns are as follows: dorsals 30–35 ($\bar{x}$ = 32.7), ventrals 39–47 ($\bar{x}$ = 42.0), femoral pores 9–13 (total 23.5), supraoculars 5 (with two specimens having 4–5). The largest specimen, an adult male, is 96 mm S-V.

Sceloporus clarki uriquensis
Tanner & Robison

Sceloporus clarki uriquensis Tanner and Robison 1959, Great Basin Nat. 19(4):75–82.
Sceloporus clarki boulengeri Hardy and McDiarmid 1969, Univ. Kansas Publ., Mus. Nat. Hist. 18(3):129–134.
Urique, 3 (BYU 1410–12) and 3 (KU 56215–17).
1 mi N Maguarichic, 9 (BYU 16890–98).
Area above Pitahaya, on the Río San Miguel, 3 (BYU 22678–9, 22682).
23 mi S 1.5 mi E Creel, Barranca del Cobre, 1 (KU 44175).

Hardy and McDiarmid (1969) examined a large series of *Sceloporus clarki* (140) from Sinaloa and three specimens (KU 56215–17) from Urique, Chihuahua. On the basis of this series, they conclude that *S. c. uriquensis* is a variant of *S. c. boulengeri*. They also implied that such a conclusion pertains to all populations inhabiting the Río El Fuerte basin. Hardy and McDiarmid (1969) did not examine the types of *S. c. uriquensis* or other available specimens from the basin. An examination of the material, as listed above, does indicate that there are differences not only in scalation but also in color pattern between *S. c. boulengeri* and *S. c. uriquensis*, which were not, apparently for lack of material, noted in their report.

The naming of a new taxon from a single specimen or a few specimens is at best hazardous; yet this is often done in the hope that the material at hand is representative of the population. The naming of *S. c. uriquensis* is a case in point, and Hardy and McDiarmid (1969), based on their data, were perhaps justified in their conclusions. In some scale patterns there is considerable overlapping, as there is in most subspecies with adjoining areas of distribution. However, in this case we are dealing with river basin isolation. Such species with the degree of variation present in *S. clarki* are particularly susceptible to character modifications arising from a reduced gene flow occurring in such instances.

The following data are derived from 17 specimens from Chihuahua, including the three topotypes (KU 56215–17): dorsal scales 28–33 ($\bar{x}$ = 29.8), ventral scales 40–47 ($\bar{x}$ = 44.0); scale rows 34–38 ($\bar{x}$ = 36.2); supralabials 4–5 ($\bar{x}$ = 4.35); infralabials, range 5–7; nasal separated from lorilabials, 12 of 26 = 46%; one scale between subocular and labial below eye, 9 of 26 = 34.6%; postmentals reduced to 2 or 4 = 100%; four supraoculars, 12 of 26 = 46%; femoral pores 11–14 ($\bar{x}$ = 12.1). Although there is considerable similarity between most of the characters of the larger Chihuahua series and the Sinaloa series (Hardy and McDiarmid 1969), some noteworthy differences do appear. The dorsals are reduced to approximately 30 scales and barely approach the lower limits of the Sinaloa series. The femoral pores are noticeably reduced and may only reach the lower limits of the Sinaloa series (14–24 per femur). In the Chihuahua series (17 specimens) the femoral pores range from 11 to 14 per femur, total 23–27 ($\bar{x}$ = 24–29). In this series the individual femoral pore counts are as follows: 4 specimens 11–12, 7 with 12–12, 4 with 12–13, 1 with 13–13, and 1 with 13–14. This range ($\bar{x}$ = 12.12) per femur barely reaches the lower limits in one series (Culiacán) listed by Hardy and McDiarmid (1969:130, Fig. 8).

In the description of *S. c. uriquensis* it is clearly stated that the femoral pores were reduced to 12–12; however, a large series of *S. c. boulengeri* was not available at the time of the description to emphasize the importance of this character. In neither study has this character been given the consideration it obviously deserved. Other scale patterns do not provide adequate distinctions to separate the two subspecies. Tanner and Robison (1959) recognized the uniqueness of *uriquensis* based primarily on the color pattern. The green head cap in males is not seen in either *c. clarki* or *c. boulengeri*. Furthermore, the dorsolateral stripe, usually present in the other subspecies, is absent or faint in *c. uriquensis*.

The reduced femoral pores, reduced dorsals, the green head cap in males, and the near absence of the dorsolateral light stripes, particularly in males, serve to distinguish *S. c. uriquensis* from other subspecies of *Sceloporus clarki*.

The distribution of *S. c. uriquensis* at present includes only the Río El Fuerte basin of Chihuahua. A specimen from Alamos, Sonora (MCZ 43253), has an increase in dorsals (33) and ventrals (51) but has reduced femoral pores (11–12). It is a juvenile male (58 mm S-V) with tannish brown color and with no indication that a green head cap was present. Intergradation may occur in the adjoining areas west of the steep escarpment of western Chihuahua.

Sceloporus magister bimaculosus Phelan & Brattstrom

Sceloporus magister Hallowell, 1854, Proc. Acad. Nat. Sci. Philadelphia 7:93.

Sceloporus magister magister Linsdale, 1932, Univ. California Publ. Zool. 38:365.

Sceloporus magister bimaculosus Phelan and Brattstrom, 1955, Herpetologica 11(1):9–10.

NW Chihuahua, south of Antelope Wells, 1 (BYU 30644).
.5 mi S Las Palomas, 1 (UTEP 3460).

We did not find that the geographical range of this species extends much below the northern edge of the state. Smith and Taylor (1950) extend the range east and south into Coahuila and Durango. It was not found throughout central Chihuahua and may occur to the east of Highway 45 where we did not collect.

Phelan and Brattstrom (1955) list a specimen (USNM 2964) from between El Paso, Texas, and Janos in northwestern Chihuahua. The distribution of this species in Chihuahua is not yet fully determined. Parker (1982) lists it for northern and eastern Chihuahua.

Sceloporus horridus albiventris Smith

Sceloporus horridus albiventris Smith, 1939, Publ. Field Mus. Nat. Hist., Zool. Ser. 26:108–10.

Urique, 6 (BYU 14304–09).
1 mi N Maguarichic, 1 (BYU 16908).
Area above Pitahaya, near Río San Miguel, 1 (BYU 22680).

The scalation is as follows: scale rows 31–38 (33.7); dorsals 31–35 (33); ventrals 31–37 (34.9); supralabials 5–5 no variation; infralabials 6–7 (6.4); femoral pores 3 or 4, total per specimen $\bar{x} = 6.38$; the largest, an adult male S-V 88.1 mm; the smallest, a hatchling, taken 13 October 1964, S-V 38 mm.

The femoral pores average approximately one more (6.4) than the series reported for Sinaloa (5.8) by Hardy and McDiarmid (1969). Other scalation patterns do not differ. The color pattern as reported by Cope, 1898 (1900) and Tanner and Robison (1959) is distinctive, with males having a red to a reddish orange head cap. This is a most conspicuous character and is reminiscent of other species having this unusual characteristic, such as *Crotaphytus*, *C. auriceps* (Utah), and *Agama a. lionotus* (Kenya). Unfortunately, some color and color patterns are lost in preserved specimens; yet such color characteristics in live individuals represent a special distinction.

Sceloporus undulatus consobrinus Baird & Girard

Sceloporus consobrinus Baird and Girard, 1853, in Marcy and McClellan, Explorations of the Red River of Louisiana, pp. 224–226.

Sceloporus undulatus consobrinus Cope, 1898 (1900), Ann. Rept. U.S. Nat. Mus., pp. 377–380.

30 mi S Ciudad Juárez, 1 (BYU 15253).
5 mi E Ricardo Flores Mágon, 1 (BYU 13387).
1 mi W Sueco, 6 (BYU 15363–8).
18.5 mi E Ricardo Flores Magón, 10 (BYU 13402, 13405, 13412–13, 15363–68).
2 mi N Colonia Juárez, 10 (BYU 13348–50, 13352, 15189–91, 15748–49, 15751).
30 mi S Ascensión, 1 (BYU 15786).
20 mi N Colonia Dublán, 1 (BYU 15787).
Mouth of Tinaja Canyon, 1 (BYU 15791).
Colonia Juárez, 10 (BYU 17017–20, 17037–42).
6 mi N Chihuahua City, 5 (BYU 15302–3, 15308, 15332, 16986).
19 mi by highway S Chihuahua City, 1 (BYU 15713).
33 mi by highway S Chihuahua City, 1 (BYU 15815).
50 mi W (by Highway 16) Chihuahua City, 3 (BYU 13826–28).
Call Canyon, near Colonia Juárez, 2 (BYU 41769–70).

The data provided by Smith (1939) for *Sceloporus u. consobrinus* are essentially the same in all characters for the Chihuahua specimens. Cole (1963) confirms the previous reports and adds valuable ecological and life history data. An examination of my field notes indicates basically the same altitudinal distribution data as that provided in the Cole report. Most of the specimens seen and collected were along the valley roads, many of them sunning on rocks and mounds of soil which had been left as the roads were constructed. In these habitats, *consobrinus* was seen repeatedly throughout central Chihuahua. Their behavior in this regard is reminiscent of other subspecies such as *u. tristichus* and *u. elongatus*.

The scale patterns (46 specimens) are summarized as follows: dorsals 37–44 (40.5); femoral pores, 11–18 on single femur, average 15.9, total per specimen 25–36, average 31.8. These data are almost identical to those provided by Smith (1938) and Cole (1963).

Sceloporus virgatus Smith

Sceloporus undulatus virgatus Smith 1938. Occ. Pap. Mus. Zool. Univ. Michigan 387:11–14.
Sceloporus virgatus Cole, 1963, Copeia No. 2:413–425.
Río Bavispe, below Tres Ríos, 1 (BYU 13435).
8 mi W Chuhuichupa, 6 (BYU 14262–6, 15486).
4 mi N Chuhuichupa, 2 (BYU 15425–6).
Cuiteco, 2 (BYU 14267–8).
Cerocahui, 1 (BYU 14605).
Between Cerocahui and W rim of Barranca del Urique, 2 (BYU 15648–9).
25 mi W Colonia Juárez on road to Tres Ríos, 9 (BYU 15442–8, 15807–8).
Meadow Valley, 1 (BYU 15715).
2 mi N Maguarichic, 1 (BYU 16916).
10 mi SW San Pedro, 7 (BYU 15487, 17030–35).
28 mi SW San Pedro, 1 (BYU 15488).

San Pedro is a ranch on the west side of the Río Papigochic. Miñaca is across the river on the east bank.

In Chihuahua *Sceloporus virgatus* can be readily distinguished from other sympatric species by its small adult size (50–55 mm S-V), distinct dorsolateral and lateral stripes, and absence of blue belly patches on all specimens. Cole (1963) lists the dorsals in 9 Chihuahua specimens as 34–40, with an average of approximately 37.2. The 33 specimens listed above are 34–39 (36.94). Our series shows the femoral pores to be 25–31 (26.85). This is slightly more than those averaged by Cole. If the two specimens from the lower Río Bavispe BYU 13435 (15–15) and 13490 (15–16) are removed, the averages for femoral pores for the two series are nearly equal. There is reason to suspect that these populations, as do other species from the Bavispe basin (e.g., *Thamnophis e. errans*), show a relationship to populations to the north. Only below Tres Ríos do we see an increase to 30 or more femoral pores. In other samples in Chihuahua, only three specimens have 15 pores and this on only one femur. The predominant pore formula is 13–13, 13–14, or 14–14. Data from the Cole study and data available to me show a north-to-south cline in the basic characters. Chihuahua specimens have an average of fewer dorsals, scale rows, and femoral pores than populations in Arizona and New Mexico.

The elevation of *virgatus* to a full species is justified not only on the basis of the characters listed by Cole (1963) but also from the fact that *virgatus* is allopatric to all members of the *undulatus* group. In our travels we found them only in the oak and oak-pine habitat, well above the desert foothills where *S. u. consobrinus* occurs. However, the small blue patches on each side of the throat do suggest a relationship to the *undulatus* group, where it has been placed with *undulatus*, *occidentalis*, *graciosus*, and *woodi* (Larson and Tanner 1975).

Sceloporus grammicus disparilis Stejneger

Sceloporus disparilis Stejneger, 1916, Proc. Biol. Soc. Washington 29:227–230.
Sceloporus grammicus disparilis Smith and Laufe, 1945, Trans. Kansas Acad. Sci. 48:332–333.
1 mi S Chuhuichupa, 8 (BYU 13927–34).
3 mi N Chuhuichupa, 2 (BYU 13937–8).
24 mi from Colonia Juárez, on road to Tres Ríos, 1 (BYU 15809).
García, 3 (BYU 32233–5).
Cienega la Prieta, 4 mi W Guachochic, 8 (BYU 22660–7).
La Mesa de Arturo, 1 (BYU 22673).

Those specimens taken north of the Río Papigochic were in timbered habitats at elevations ranging up to 8,000 feet. South of Chuhuichupa the habitat was near old pine stumps and fallen logs. The largest specimens were 50 mm in S-V length.

Scale patterns ranged as follows: dorsals 61–73 and femoral pores 12–17 (total average 27.2). Those north of the Río Papigochic have a reduced series of dorsals 61–70 ($\bar{x} = 65.4$) in contrast to those in the Río Fuerte basin at 64–73 ($\bar{x} = 69.0$). The pores are also reduced in the northern populations 12–14 (total $\bar{x} = 26.0$). Color patterns did not seem to vary.

The variations in *Sceloporus grammicus* are not well known. At present this species is being studied throughout its total range. Therefore, in this study only the obvious variations in the Chihuahua specimens are reported, with no attempt to compare them to southern populations.

Sceloporus poinsettii Baird & Girard

This large, attractive *Sceloporus* occurs from southern New Mexico and Texas south in Mexico through Coahuila to Nuevo León to the east and throughout Chihuahua and Durango to northern Zacatecas. The most western locality is in extreme eastern Sonora at Nutria Creek, a small tributary of the Río Bavispe. Within this large area of distribution there are three subspecies presently recognized. The nominate subspecies, *poinsettii*, as it is now understood, occurs in the north and east, New Mexico, Texas, northern Chihuahua, northeastern Sonora, northern and eastern Coahuila, and Nuevo León. To the west *macrolepis* is in northern Zacatecas and the highlands of western Durango. In Chihuahua, considerable intergrading occurs and will be discussed below.

Sceloporus p. polylepis appears to be a smaller representative of the species and to inhabit the lower foothills and valleys of southern Chihuahua and east central and northeastern Durango. It may also occur in southwestern Coahuila. Apparently, the distribution of this subspecies is entirely within the enclosed basins of north central Mexico.

Specimens from areas west and south of Chihuahua City show considerable variation both in the number of dorsal scales and femoral pores. Except for a population in southwestern Chihuahua, the area consists of populations with variable characteristics that are obviously related to the other subspecies both to the north and south. The population in the Río Oteros basin has variations that show intergradation but also possesses destructive characters.

Sceloporus poinsettii poinsettii
Baird & Girard

Sceloporus poinsettii Baird and Girard, 1852a, Proc. Acad. Nat. Sci. Philadelphia, 6:126–127.

Sceloporus p. poinsettii Smith and Chrapliwy, 1958, Herpetologica 13:267–270.

Colonia Dublán, 6 (BYU 401, 1323–5, 15386–7).
11.5 mi SE Nuevo Casas Grandes, 1 (BYU 13853).
14 mi W Ricardo Flores Magón, 1 (BYU 15334).
60 mi S Gallego (on Highway 45), 1 (BYU 13926).
4 mi N Chuhuichupa, 1 (BYU 15424).
25 mi W Colonia Juárez on road to Tres Ríos, 4 (BYU 15436–9).
Río Chico, 1 (BYU 15753).
Cuesta el Toro, 5 mi S Gómez Farías, 2 (BYU 15692–3).
NW Chihuahua (W Janos), 1 (BYU 30645).
7 mi E Buenaventura, 1 (BYU 40048).
15.4 mi S Villa Matamoros, 2 (BYU 41777–8).
Sonora: 4 mi E Río Nutria, 1 (BYU 13491).
Coahuila: 15 mi SE Saltillo (Highway 57), 8 (BYU 36243–49, 36399).
New Mexico: Elephant Butte Lake, Sierra Co., 1 (BYU 30520).
Texas: Pine Canyon, Chisos Mts., Brewster Co., 1 (BYU 40376).
Intergrading populations, all in south central Chihuahua: 10 mi W San Francisco del Oro, 6 (BYU 15679–83, 15710); 1 mi NE San Pedro on Río Papigochic, 9 (BYU 15685–90, 17053–5); 20–27 mi NE San Juanito on road to La Junta, 4 (BYU 41081–4); 25.5 mi S Creel (La Bufa Road), 5 (BYU 17138–42); 62 mi W Chihuahua City, 5 (BYU 13861–5); San Pedro, 2 (BYU 14523, 15771); 50 mi W Chihuahua City, Highway 30, 14 (BYU 13812–25); 18 mi SW San Pedro, 1 (BYU 15475).

Except that *p. poinsettii* and *p. polylepis*, as presently known, are widely separated, one would find difficulty in devising a key to separate them. Smith and Chrapliwy (1958) based the distinction on small, more numerous dorsals and a smaller body size (S-V 96 mm). In northern Chihuahua and the United States populations of *poinsettii* have larger dorsals (32–36). It is not until populations in central Chihuahua are reached that the dorsals are reduced to 29–31, perhaps an indication that an influence of *p. macrolepis* is affecting the number of dorsals. The specimens from Chihuahua City and west in the Conchos and Papigochic basins are intermediate in the basic characters presently used. The series from 10 mi W of San Francisco del Oro have dorsals 28–31, lower than the average for the intergrade series (Table 1) but not yet to be included in the *p. macrolepis* series. A single specimen from 27 miles south of Parral is here listed as a *p. polylepis*. It does, however, have more femoral pores (25) than others from Durango (19–23) and may indicate a relationship to the population in central Chihuahua.

Sceloporus p. poinsettii is the most variable of the subspecies (Table 1). It is also the one with the greatest area of distribution. The series (17) from northwestern Chihuahua has more dorsals with 31–36 ($\bar{x} = 33.2$) than those from the northern and eastern populations (13), with 30–36 ($\bar{x} = 31.85$). Obviously, these series are too small to be considered reliable but do show trends in both characters listed in

TABLE 1. Dorsal scales and femoral pore variations in the subspecies of *Sceloporus poinsettii* Baird & Girard.

Subspecies	No.	Dorsals	Femoral pores		Distribution
poinsettii	30	30–36 (32.63)	16–25 (21.03)	20 or more 77%	New Mexico, Texas, Chihuahua, Coahuila
macrolepis	14	26–28 (27.85)	20–28 (23.80)	20 or more 100%	Durango and Zacatecas
polylepis	9	31–34 (33.22)	18–25 (21.37)	20 or more 78%	Chihuahua and Durango
robisoni	14	29–32 (30.42)	14–21 (18.64)	20 or more 85%	Chihuahua
Intergrades	43	30–33 (32.76)	18–28 (22.60)	20 or more 92%	Chihuahua

Table 1. In the northern population of Chihuahua, from the lower eastern foothills and valleys, nine specimens from west of Colonia Juárez (7,000–8,000 feet) have 33–36 ($\bar{x}$ = 34.4) dorsals, in contrast to the Durango mountainous populations (*p. macrolepis*). In these two mountain populations there is a difference of 7+ dorsals (*macrolepis* 27.85 [south] and *poinsettii* 34.44 [north]); this perhaps explains the intermediate (intergrading) populations in south central Chihuahua.

Sceloporus p. macrolepis
Smith & Chrapliwy

Sceloporus p. macrolepis Smith and Chrapliwy, 1958, Herpetologica 13:267–271.
West of Ciudad Durango, 2 (BYU 41325, 41368).
4 mi W Ciudad Durango, 1 (BYU 40100).
East of Ciudad Durango, 1 (BYU 41327).
32.5 mi W Ciudad Durango, 4 (BYU 14533–5, 15376).
22 mi S Sombrerete, Zacatecas, 6 (BYU 13855–60), paratypes.
Belleza, 1(USNM 47417).
Guachochic, 6(USNM 13855–60).

Populations in southwestern Chihuahua are intergrades between *macrolepis* (south) and *poinsettii* (north). (See Table 1 and the discussion above). I did not see the specimens reported by Smith and Chrapliwy for Belleza and Guachochic, Chihuahua.

There are color and color pattern differences between the specimens from south of Sombrerete, Zacatecas, and those from near the type locality in western Durango. In *macrolepis* the eye is circled by a bright red, which is most noticeable in living specimens. Also, the cross banding is faint, and a rustic color predominates on the nape and back. Durango specimens are dark without the red around the eyes and with cream-colored bands across the body. In S-V length BYU 13857 (Zacatecas) = 117 mm and BYU 40100 (Durango) = 108 mm.

Sceloporus p. polylepis
Smith & Chrapliwy

Sceloporus p. polylepis Smith and Chrapliwy 1958, Herpetologica, 13:267–271.
27 mi S Parral, Chihuahua, 1 (BYU 15652).
10 mi W Gómez Palacio, Durango, 3 (BYU 40064–6).
25 mi S Gómez Palacio, 1 (BYU 40115).
6 mi NE Pedriceno Highway 49, 3 (BYU 36236–8).
25 mi S Torreón Highway 49, 1 (BYU 36240).
140 mi S Torréon Highway 49, 1 (BYU 36241).

Specimens from near the type locality have dorsals 35–37; the one from Chihuahua 34 and the one 140 mi S Torreón only 30. Both are intergrades between *polylepis* and *macrolepis*, and in both cases the specimens are near the area of distribution for *macrolepis*. The data now available suggest that the subspecies *polylepis* is restricted to the low plains extending from southeastern Chihuahua to northeastern Durango. This distribution also suggests that it may occur in adjoining Coahuila.

The largest adults (40064, S Gómez Palacio and 36240, S Torreón) have S-V length of 82 and 83 mm. If these size data and those presented by Smith and Chrapliwy (1958) are representative of the populations of this subspecies, then it is indeed a small representative of the species.

Sceloporus poinsettii robisoni, subsp. n.

HOLOTYPE.—BYU Bean Mus. Nat. Hist. 14287, adult male, Cuiteco, Chihuahua, collected 19 July 1958, by W. W. Tanner and W. G. Robison.

PARATYPES.—BYU 14273–5, 14288–9 topotypes; BYU 14602, 15667–9, 15670, Cerocahui; BYU 17070–2, along road 4–8 mi SE Maguarichic.

DIAGNOSIS.—A southwestern Chihuahua subspecies of *poinsettii* with reduced femoral pores, 85% with 20 or less, compared to

TABLE 2. Variation in three head scale patterns.

Subspecies	No.	Nasal to lorilabials percent	Labiomentals to mental percent	Median scale anterior to interparietal percent	Adult size
poinsettii	17	west 90 east 44 71	12	100	82–120 mm
macrolepis	14	65	7	38	101–117 mm
polylepis	9	90	0	90	78–99 mm
robisoni	14	90	50	57	85–113 mm
Intergrades	59	85.5	20	90	85–115 mm

75–100% with 20 or more in other subspecies; dorsals low, 29–32; postmentals not in contact with infralabials; and adults large, 110–115 mm S-V.

DESCRIPTION OF TYPE.—A young adult male, S-V 88.5 mm, total length 175 mm, dorsals 29, ventrals 47, scale rows 37, femoral pores 7–7; head scalation much as in *S. p. poinsettii*, most patterns variable, two rows of supraoculars, lorilabials contact nasal on one side; labiomentals contact mental; postmentals not in contact with infralabials; anterior dorsals, two parietals, and four enlarged scales surround the interparietal.

Black collar 3 scales across medially, edged anteriorly by 2 scales of cream color and edged posteriorly by one light scale row, dorsum of body not distinctly barred; tail with 6 distinct rings; lateral belly blue patches edged medially with darker blue, sides of throat and chin suffused with light blue, separated medially by a lighter area.

VARIATION.—The subspecies of *Sceloporus poinsettii*, as noted in Table 1, are variable in the numbers of dorsal scales and femoral pores. Most noticeable is the consistently low number of pores of *robisoni*. Of the type series (14), only 2 specimens have a total of 21, 3 have 20, and 9 less than 20. In the dorsal head scales there is little uniformity, except that in all *poinsettii* subspecies the frontal is widely separated from interparietal, either by one or several small scales or by enlarged scales extending anterior from the parietals to the suture anterior to the interparietal. Table 2 summarizes the variation observed in three head scale patterns. Smith and Chrapliwy (1958) referred to the relationship of the labiomentals to the mental, frontal to interparietal, and size of adults. Aside from the fact that *macrolepis* has larger and fewer dorsals and *polylepis* has smaller and more dorsals than other subspecies or populations examined, the relationships illustrated in Table 2 indicate additional differences not presented in the original description. In *p. polylepis* the labiomentals do not contact the mental and in size the adults (5), except for one, were less than 90 mm in S-V. They are more slender and less robust than other subspecies. These data strongly suggest that *Sceloporus poinsettii* is undergoing differential environmental pressures from its desert to foothill to mountain habitats and thus may represent a rapidly evolving species.

Sceloporus jarrovii jarrovii Cope

Sceloporus jarrovii jarrovii Cope, 1875b, U.S. Geological and Geographical Surveys, W 100th Meridian 5:569.

Colonia García, 4 (BYU 2956, 1328–30).
25 mi from Colonia Juárez on road to Tres Ríos, 13 (BYU 15440–1, 15599–600, 15792, 15811, and 7 mature embryos 32578–84).
Black Canyon, west of Chuhuichupa, 11 (BYU 142767–82, 37632–35).
3 mi N Chuhuichupa, 21 (BYU 13903–7, 13935–6, 15413–14, 15416–23, 15469–72).
Meadow Valley, 2 (BYU 15716, 15743).
North end of Blues Mountain–Gavilancito Sawmill, 2 (BYU 13596 and 15709).
Río Chico, 3 (BYU 15754–6).
Cuesta el Toro, 5 mi S Gómez Farías, 2 (BYU 157894–5).
4 mi SE Creel, 12 (BYU 14520–21, 15587–96).
1 mi NE Bocoyna, 3 (BYU 15476–8).
Cerocahui, 12 (BYU 14597–601, 15474, 15645–7, 15671–3).
Cuiteco, 10 (BYU 14270–2, 14290–3, 15657–8, 15664).
10 mi SW San Juanito, 7 (BYU 15796–802).
1 mi W La Lanja, 4 (BYU 16873–6).
26 mi W San Juanito, 7 (BYU 16960–6).
22.5 mi S Creel (along La Bufa road), 4 (BYU 16947–50).
25.5 mi S Creel (along La Bufa road), 16 (BYU 17654–5, 17659, 17661–2, 17664, 17666, 17668–70, 17672–4, 17759, and 17021–2).
4–8 mi SE Maguarichic, 14 (BYU 17056–69).
16 mi NE San Juanito, 4 (BYU 17024–7).
20 mi SW Colonia Juárez, 2 (BYU 20973–4).
Carmen Bridge (La Bufa road), 1 (BYU 22719).
1 mi W Carmen Bridge, 4 (BYU 22668–71).
La Mesa de Arturo, 1 (BYU 22672).
Turkey tanks SW Colonia Juárez, 1 (BYU 41760).]

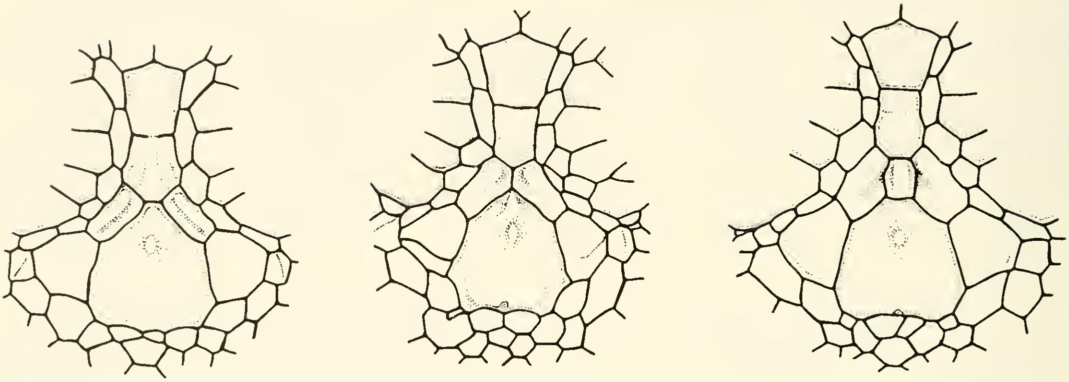

Fig. 4. Dorsal head scale variations in *Sceloporus j. jarrovii*. See text for explanations.

We found this species to be widespread in all suitable habitats throughout the western mountains. It was commonly seen in areas where rocky outcroppings occurred and on boulders strewn along roads. It is apparently replaced in the foothills and central valleys by *S. u. consobrinus* and *S. poinsettii*.

There is noticeable variation within some populations in the number of dorsal scales. This variation is reflected in samples from different basins; for example, in Cerocahui 12 specimens have 39–44 ($\bar{x}$ = 41.1), and specimens 7 to 10 mi SE San Juanito have 37–40 ($\bar{x}$ = 38.8). However, when all specimens from south of the Río Papigochic are included, the following data are obtained: 96 specimens 37–45 ($\bar{x}$ = 40.4). This is generally true for specimens north of the Río Papigochic in which 52 specimens range from 37–44 but average 41.2 scales in the dorsal series.

The femoral pores vary from 12 to 18 per femur and show population variation as in the dorsals but with the southern population tending to have higher numbers than those north of the Río Papigochic. The head scales are also variable. The relationship of the interparietal to the frontal, as an example, shows the following as illustrated in Figure 4. In A, 61 specimens or 41% are as illustrated; B, 34 specimens are 23%; and C, 53 specimens are 36%. Other dorsal head scales show some pattern variations but were not examined.

The labials varied little with the upper labials, 4–4 rarely 5, and the lower labials usually 6–6 but occasionally 5 or 7. In 51% of the total series the nasal was in narrow or broad contact with the anterior lorilabial. The most stable pattern was that of the sublabials, which do not contact the mental, thus permitting contact of the postmental and the first infralabial. In 148 specimens only 3 submentals contact the mental on one side.

Since collecting was done from May to October, the BYU series includes all age groups. On 28 June 1958, a gravid female, 75 mm S-V, was collected 25 mi W of Colonia Juárez. She contained 7 well-developed embryos, 4 females and 3 males, ranging in S-V length from 22 to 24 mm. All color and scalation patterns were fully developed. In the latter, the hemipenes were fully everted. At this locality on the same day, 3 young were collected and measured 25, 26.5, and 27 mm in S-V length. These data indicate that birth in the mountains occurs in middle to late June. On 5 July 1958, at Black Canyon, 8 mi W of Chuhuichupa, 4 young were collected. These measured 24.6, 28, 29, and 31 mm S-V. Four juveniles collected at Cuiteco on 28 July 1958 measured 42–44 mm in S-V.

Elevation may be a factor since specimens taken at about the same dates in 1957 and 1958 at Chuhuichupa and near Creel (8,000 feet) were smaller (35–37 mm S-V) than those taken at a lower elevation at Cuiteco. By October the year's young are 50–60 mm S-V.

Sceloporus slevini Smith

Sceloporus scalaris slevini Smith, 1937, Occ. Pap. Mus. Zool. Univ. Michigan 361:3–4.

Sceloporus scalaris Thomas and Dixon, 1976, Southwestern Nat. 20(4):523–536.

Madero Canyon (Tureze), 1 (BYU 1326).
Cerocahui, 3 (BYU 14603–4, 15489).
2 mi S Creel, 1 (BYU 15597).
3 mi N Chuhuichupa, 4 (BYU 13799, 15717–9).
Meadow Valley, 1 (BYU 15714).

12 mi SW Miñaca, 2 (BYU 15506, 15770).
6 mi S San Juanito, 1 (BYU 17096).

In Chihuahua this species is found only in the western mountains at elevations ranging from about 6,500 to 8,000 feet. Records from the lower central ranges and valleys, such as Chihuahua City or 30 mi S El Paso (Smith 1937), were not confirmed by our collecting in these areas. Their habitat of grassy, low-growing herbs and brush did not make for easy collecting and consequently large series were not taken.

All adults in this series varied in S-V length from 46 to 56 mm. The smallest is a male and the largest a female. Dorsals were 40–47 ($\bar{x}$ = 42.92), femoral pores 12–16 per femur or total pores 25–30 ($\bar{x}$ = 27.8). Other scale patterns were within those listed by Smith (1939). Color patterns showed some individual variation but were well within patterns previously established for the subspecies.

Except for one specimen, BYU 13799, taken on 27 August 1957, all were collected during July. Three of those from north of Chuhuichupa (2–6 July 1958), one from Cerocahui (BYU 15489, 13 July), and one from south of Creel (BYU 15597, 20 July) were gravid females. They ranged in size from 47 to 55 mm S-V and contained 4–7 eggs. The largest contained 7 eggs, and the smallest 4. The larger eggs in each individual measured 6–11 mm. All were heavily laden with yolk and the larger ones were compacted, except in the specimen with only 4 eggs, thus accounting for the round rather than elongated shape. The larger eggs were in specimens taken in late July.

We saw no hatchlings and suspect that eggs are laid in late July or early August. Hatchlings would seem to appear in late August or September.

Sceloporus nelsoni barrancorum
Tanner & Robison

Sceloporus nelsoni coeruleus Tanner and Robison, 1959, Great Basin Nat. 19(4): 79–81.
Sceloporus nelsoni barrancorum Tanner and Robison, 1962, Herpetologica 16(2): 114.
Sceloporus nelsoni: Hardy and McDiarmid, 1969, Univ. Kansas Publ., Mus. Nat Hist. 18(3): 136–38.

Urique, 10 (BYU 14315–20 and 14322–5).
Teradakwa Creek near Río Urique, 1 (BYU 22721).
3 mi NE Temoris, 1 (KU 51795).
1.5 mi Tocuina, 14 (KU 47426–28, 51060–70).
23 mi S 1 1/2 mi E Creel, Barranca del Cobre, 1 (KU 44293).
6 km NE El Fuerte, Sinaloa, 7 (KU 78669–75).
16 km NNE Choix, Sinaloa, 9 (KU 73728).
9 mi SE Alamos, Sonora, 9 (KU 47537–45).
8 mi SE Alamos, Sonora, 4 (KU 49702–5, 91498, 176533).
Guirocoba (Sonora), 1 (MCZ 37855).
Río Mayo Guasaremos (Sonora), 1 (MCZ 43276).
Other material examined: Sinaloa: 32 mi SSE Culiacán (KU 37773), 1.5 mi E Santa Lucía (KU 44833–39), 1 mi E Santa Lucía (KU 44840–49), 12 mi N Culiacán (KU 4485), 1 mi SE Camino Real, Río Piaxtla (KU 63706–8), 44 km ENE Sinaloa (KU 69932), 6 km E Cosala (KU 73729), San Ignacio (KU 73730–32), 5 km SW El Palmito (KU 75582), 8 km N Carrizalejo (KU 78676–77), 5 km SW San Ignacio (KU 78678–79), 8 km N Villa Unión (KU 80731), 13 mi ESE Badiraguato (KU 83400), 5 mi E Presa Sanalona (KU 93479). *Sceloporus n. nelsoni*, type USNM 47676 and paratypes USMN 18979, 47271, 47273–5, 47629, 47690–1. Nayarit: 18 mi S Acaponeta (BYU 14383–4). Jalisco; 3 mi N Guadalajara (KU 27202–3).

Hardy and McDiarmid (1969) examined a series of 72 specimens, 56 from localities in Sinaloa and 16 from southwestern Chihuahua. They did not study specimens from the type locality nor from the type series reported by Tanner and Robison (1959). A reexamination of the data from the type series of *n. nelsoni* and *n. barrancorum* and an evaluation of the material now available from or near the type localities indicates that a further examination of the variations in these subspecies is justified.

In the original description of *S. n. barrancorum* some characters were not clearly defined. Therefore, it appears appropriate and necessary to diagnose and redescribe *S. n. barrancorum* and provide a key for the identification of the subspecies. This can now be done based on a larger series from both the northern and southern populations.

DIAGNOSIS.—*Sceloporus n. barrancorum* is smaller than *S. n. nelsoni*, S-V of 30 adults, male, 54–60.0 ($\bar{x}$ = 56.5 mm), female 50.5–55.0 ($\bar{x}$ = 52.6 mm) in contrast to specimens from near Santa Lucía and other areas near the type locality of *n. nelsoni* at Plomosas, Sinaloa; males, 58.0–68.2 ($\bar{x}$ = 62.84 mm) and females 56.1–59.1 ($\bar{x}$ = 57.25 mm); enlarged postanal scales present, color pattern in males with the ventral surface (gulars and belly) a deep blue, no white except a small white spot near each shoulder, dorsolateral stripes faint or absent, venter of adult females

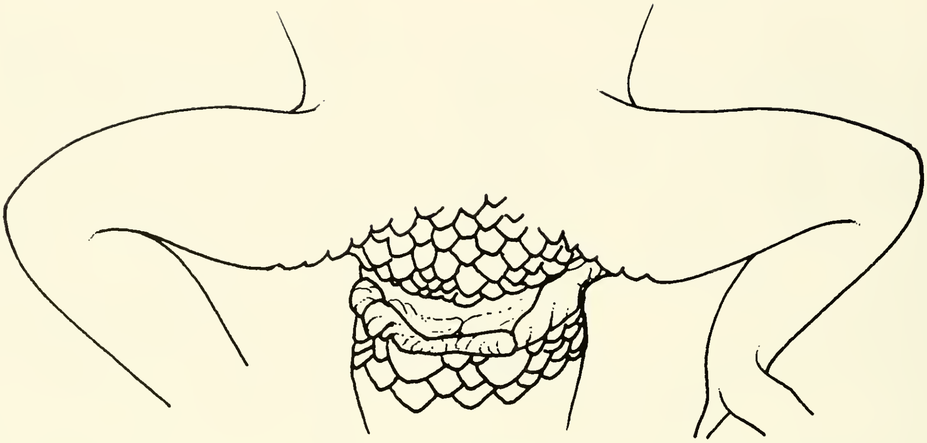

Fig. 5. Paratype of *Sceloporus n. barrancorum* (BYU 14317) showing the enlarged postanal scales.

with pale blue laterally and edged medially by a narrow stripe of dark blue, blue on belly in females separated by a narrow median light stripe, which is absent in males.

Description and Comparison.—Some characters that seemed important previously are now, based on added material, obvious variations. The head scales do show variations but not consistent in any one pattern, and the lamellae of the fourth toe do not vary. Other characters such as adult size, color patterns, and enlarged postanal scales represent significant differences between *nelsoni* populations from southern Sinaloa and Nayarit and populations in northern Sinaloa, southern Sonora, and southwestern Chihuahua.

The description of *S. n. barrancorum* was based on the type series (10 specimens) and compared with the type series of *S. n. nelsoni* at the USNM and two specimens from 18 mi S Acaponeta, Nayarit. In the study by Tanner and Robison (1959) it is clearly stated that the northern populations (southwestern Chihuahua) were smaller than typical (type series) *nelsoni*. An examination of the data presented by Hardy and McDiarmid (1969) indicates that their analysis of size data included juvenile specimens. Such data are not representative of the actual adult size in a population. I have examined the 19 specimens seen by Hardy and McDiarmid (1969) from Villa Unión (KU 80731), El Palmito (KU 75582), and Santa Lucía (KU 44833–39 and KU 44840–49). My measurements of S-V of 14 adult males of this series range from 58.0 to 68.2 mm and average 62.84 mm, in contrast to their measurements, 42–65 ($\bar{x}$ = 58.0). Although Hardy and McDiarmid (1969:136) state that "the maximum snout-vent length is slightly smaller in Chihuahua and northern Sinaloa than in southern Sinaloa," they fail to corroborate this observation in their data (p. 137, Table 4). In small species, such as *nelsoni*, an increase of 4–5 mm in the S-V of adults substantially increases the body mass and is obvious by inspection. By eliminating juveniles and segregating males and females, a size differential between populations (subspecies) is evident.

The presence or absence of enlarged postanal scales was not considered in the Hardy-McDiarmid (1969) study. Cochran (1923:186) states that males have "slightly developed post-anal scales." Smith (1939:364), in the diagnosis of the species, states that there are "no enlarged postanals in males." In the type series of *S. n. barrancorum* all males (5) have enlarged postanals (Fig. 5). In the series from Santa Lucía, Sinaloa (KU 44833–44849), only one male has slightly enlarged postanals. I have not examined the type series of *nelsoni* for this character. Smith lists 38 specimens with all but 3 from localities near or south of Mazatlán in southern Sinaloa, Nayarit, and Jalisco. That he could not find enlarged postanals is not surprising, since this character apparently becomes more prominent in specimens at or north of Culiacán. Most adult males I have seen from northern Sinaloa (El Fuerte and Choix), southern

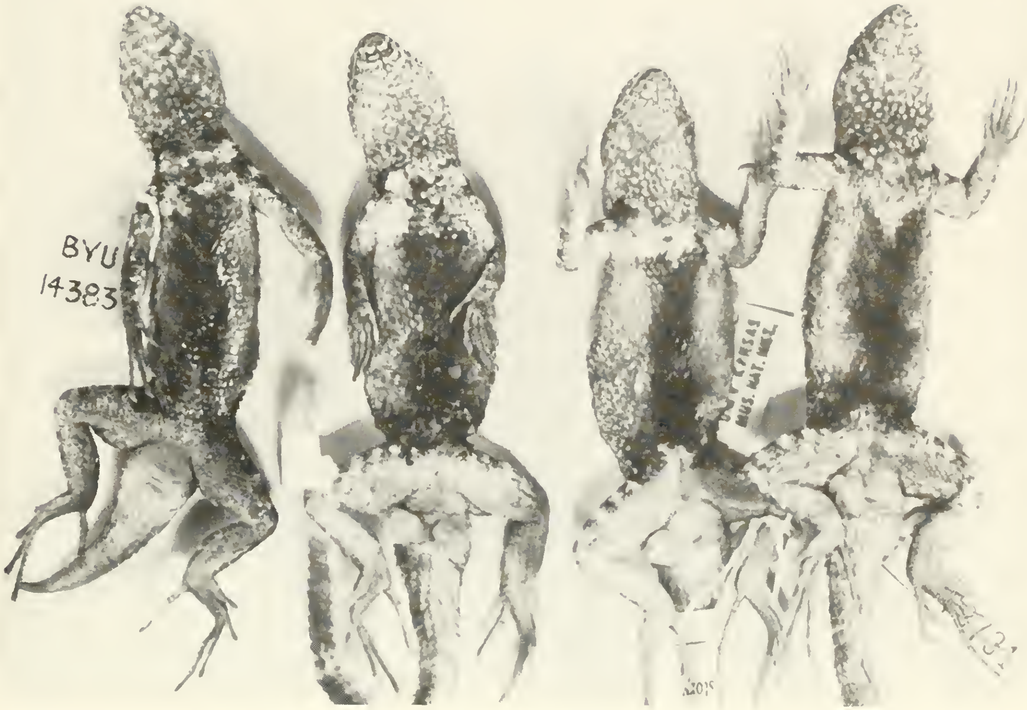

Fig. 6A. Four specimens of *Sceloporus n. nelsoni* from 18 mi S Acaponeta, Nayarit (BYU 14383), 1 mi E Santa Lucía (KU 44845), and San Ignacio, Sinaloa (KU 73730–31), depicting the basic ventral color pattern of the southern subspecies.

Sonora (near Alamos), and southwestern Chihuahua have the postanals enlarged.

Color patterns in the two subspecies are variable but distinct, with males of *S. n. barrancorum* having an intensive blue covering the entire venter from gulars to groin, and only small white spots medial to the shoulders (Fig. 6A). Males from southern Sinaloa have considerable white or cream coloring between the front legs and on the adjoining gulars. In some the blue belly patches are separated by a narrow mid-ventral light area not seen in males of the northern subspecies (Fig. 6B).

The dorsal color pattern for males of *S. n. barrancorum* is as follows: two faint dorsolateral stripes, with the area between heavily pigmented with dark bluish brown of approximately the same color as the area immediately lateral to the stripes. Females are less pigmented, the dorsal gray not contrasting with the gray below the dorsolateral lines.

In *S. n. nelsoni* there is less bluish green in the dorsal pattern. The dorsolateral lines are more distinct, and the dorsal area between the lines is a lighter brownish gray than the lateral area. As in the females of northern populations, there is less pigmentation, giving a gray pattern.

The following scale characteristics are based on the series of 17 specimens from near the type locality of *S. n. nelsoni* and contrasted with a series of *n. nelsoni* from near Mazatlán and the type series of *S. n. barrancorum* from Urique, Chihuahua. At or near the type locality of *n. nelsoni* the dorsals in the 14 male specimens range from 35 to 39 ($\bar{x}$ = 37.06). The series from near Mazatlán range from 36 to 40 ($\bar{x}$ = 37.89). The series from Urique range from 38 to 43 ($\bar{x}$ = 39.5). In the femoral pores in the same order the range is 31–39 ($\bar{x}$ = 33.82). The intermediate series is 29–40 ($\bar{x}$ = 34.10) and the Urique series 34–38 ($\bar{x}$ = 36.82). Other head scale characteristics show little modification between the southern and the northern series except that there is a noticeable variation in the size of the large scale immediately posterior to the inter-

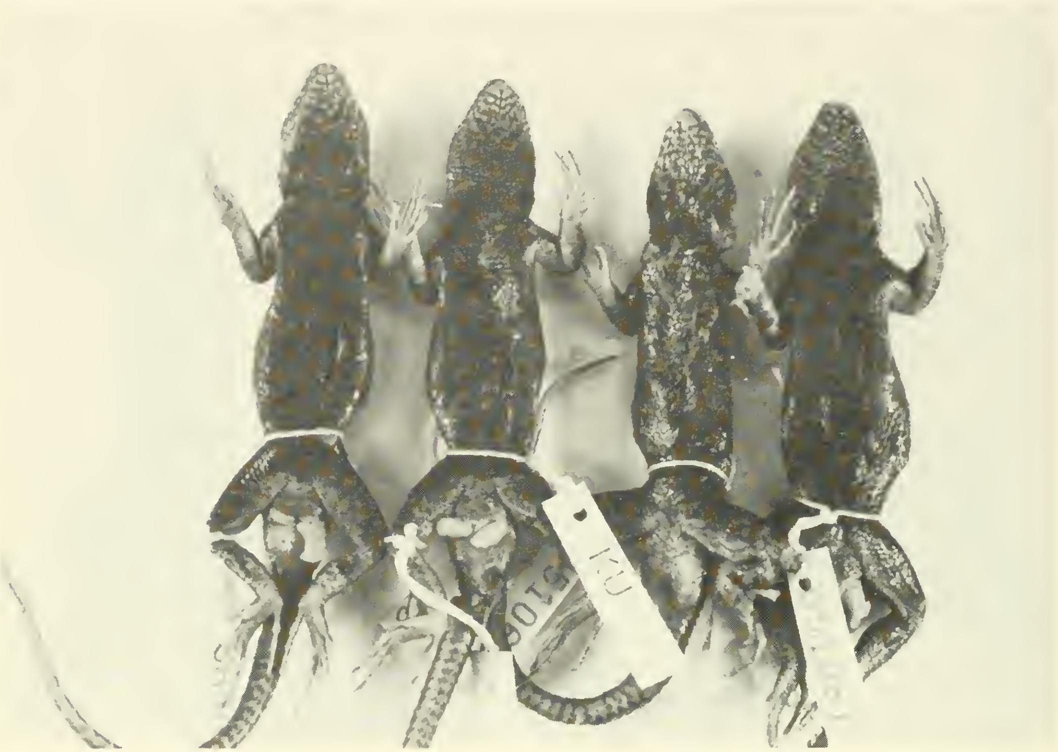

Fig. 6B. Four specimens of *Sceloporus n. barrancorum* (KU 51065, 51069, 51060, and 51067) from 1 1/2 mi SW Tocuina, Chihuahua, showing the dark (blue in life) venter from chin area to groin.

parietal. The figure in the original description of *S. n. barrancorum* (Tanner and Robison 1959, Fig. 2, original description *S. n. coeruleus*) depicts a scale much larger than the adjoining ones. This size differential is maintained in approximately 90% of the specimens designated above as *S. n. barrancorum*. In *S. n. nelsoni* this scale is reduced in size and in many specimens is the same size as or subequal to the surrounding scales. In these subspecies, as well as in other species where gradual intergrading of characters occurs, there are the expected clinal variations between the subspecies.

REMARKS.—Apparently the specimens referred to by Smith (1939) from Guirocoba, Sonora (MCZ 37855), and Río Mayo, Guasaremos, Sonora (MCZ 43276), and the specimen from Culiacán, cited by Cochran, were not seen by Hardy and McDiarmid (1969). The two Sonora specimens are identical in both scale and color pattern to the type series of *S. n. barrancorum*. That Smith (1939) did not consider the data based on three specimens (widely separated geographically) to be sufficient to establish or warrant subspecific recognition of the northern populations is not surprising. Only one of the three specimens (MCZ 37855, an adult male) would have provided the basic data for comparison with the southern populations of *nelsoni*.

Key to the Subspecies

1. Adult males with enlarged postanal scales; gulars and entire venter a deep blue (except for two small cream-colored spots near shoulders); adults smaller, males 54–60 mm, females 50–55 mm in S-V length . . . . *S. n. barrancorum*

— Adult males usually without enlarged postanals; a large area of light (white to cream) color between front legs separating the blue of the gulars and the belly; adults larger, males 58–68, females 56–59 mm in S-V length . . . . . *S. n. nelsoni*

Genus *Urosaurus*

Urosaurus ornatus Baird & Girard

The *ornatus* complex in Chihuahua is not well represented by specimens, nor are the subspecies clearly defined. A lack of specimens has made it difficult to determine distribution parameters for the subspecies that

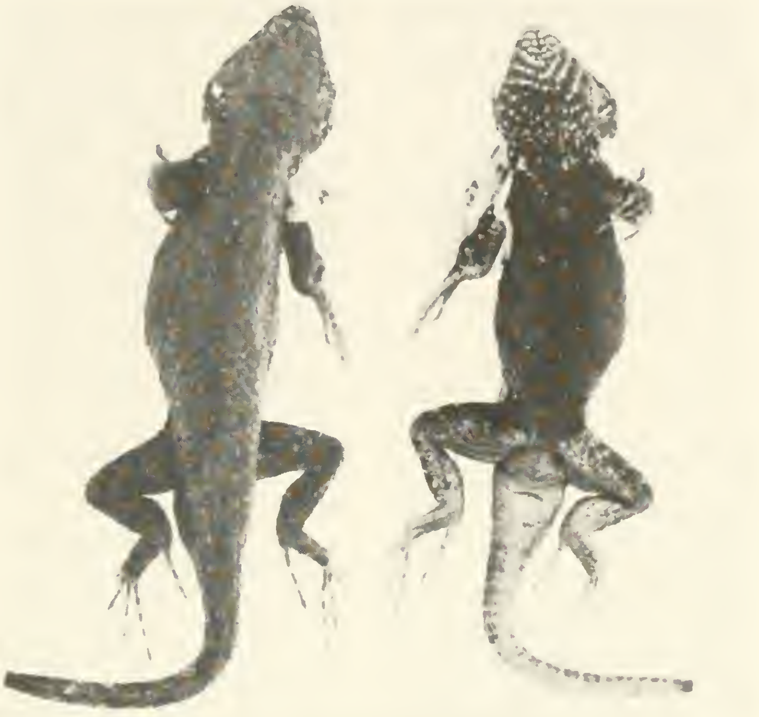

Fig. 6C. Type of *S. n. barrancorum* (BYU 14316), dorsal and ventral views.

have been reported for the state. Based on the material at hand, literature records, and the available keys (Smith and Taylor 1950), the following subspecies should occur in northern and central Chihuahua: *Urosaurus o. schmidti* Mittleman, *Urosaurus o. caeruleus* Smith, and *Urosaurus o. linearis* Baird. The latter may occur only in extreme northwestern Chihuahua. Specimens of *linearis* are not available, and its relationship to other subspecies (*caeruleus, schmidti,* and *schottii*) as well as its distribution must be established before it can be recognized. In southwestern Chihuahua, *Urosaurus bicarinatus tuberculatus* Schmidt occurs. Tanner and Robison (1959) examined the type of *Urosaurus unicus* Mittleman, type locality Batopilas, Chihuahua, and determined it to have the same basic characteristics as *Urosaurus b. tuberculatus*.

Mittleman (1940) described *Uta o. schmidti* and listed a specimen (MCZ 45589) from Colonia García, Chihuahua, as a paratype. While I am not questioning it as a representative of the subspecies, I doubt that it came from a mountain habitat such as García. In 1941 Mittleman placed *U. o. lateralis* as a synonym of *U. o. schottii* Baird. Hardy and McDiarmid (1969) recognized the subspecies *lateralis* as occurring in Sinaloa NNE of Choix, a locality near southwestern Chihuahua. Bogert and Oliver (1945), based on the study of Oliver (1943), recognized *U. o. lateralis*, rather than *U. o. schottii* Mittleman, as occurring in Sonora. Although I am unaware of specimens of the subspecies *U. o. lateralis* from southwestern Chihuahua, it undoubtedly occurs, as do many other species, as distributional extensions along the rivers of the Río Fuerte basin.

To fully understand the systematics of *Urosaurus ornata* and its subspecies would require a major study, which is beyond the scope of this study. The species and subspecies listed here are based on limited material from Chihuahua and, therefore, on my best judgment of the available specimens.

Urosaurus ornatus caeruleus Smith

Uta caerulea Smith, 1935, Univ. Kansas Sci. Bull. 22:172–178, pl. 26.

Urosaurus ornata caeruleus Mittleman, 1942, Bull. Mus. Comp. Zool., 19:136–137, pl. 9.
Colonia Dublán, 4 (BYU 1327, 2957, 3711–12).
18.5 mi E Ricardo Flores Magón, 2 (BYU 13403–4).
45 mi S Gallego (Highway 45), 1 (BYU 14157).
6.5 mi N 1.5 W Chihuahua City, 1 (BYU 15825).
La Cruz, 15 mi NNW Camargo, 1 (UTEP 3580).
24 mi (air) NNE Ascensión, 4 (UTEP 3563–6).
14 mi SE Janos, 1 (UTEP 4269).
6 mi NE Janos, 1 (UTEP 4270).
10 mi SSE Cd. Chihuahua, 1 (UTEP 4599).
16.3 mi (by Hwy 16) NE Aldama, Puerto de Gómez, 2 (UTEP 9212–13).

The characteristics of the above specimens are well within those established by Smith (1935). In adult males (S-V 42–50 mm) the entire venter is a vivid sky blue, with spots of blue on the base and lateral sides of the tail. In small or subadult males the blue is less intense and faded at the edges. The venter of females is without blue. Dorsal color pattern consists of seven irregular cross bars from nape to groin. The dorsal color is heavily pigmented between the bars, giving a melanistic appearance.

All of the scale patterns are within those set forth in the original description (Smith 1935). The ventrals, gular fold to anus are 57–68 ($\bar{x}$ = 61.7). Some scale patterns will be compared to other populations discussed below. In all but a few the head is slightly longer than wide, but less so than in two specimens of *schmidti;* extremes are: length 9.4 to width 7.5 and 9.6 to 9.8 mm. Other specimens range between these extremes. Femoral pores range from 9 to 13 and total 18 to 27 per individual. Two of the specimens are hatchlings with a snout-vent of 20.5 mm (BYU 14157) and 24.5 mm (BYU 15825). They were collected 13 August 1957 and 28 July 1958.

Urosaurus ornatus schmidti (Mittleman)

Uta ornatus schmidti Mittleman, 1940, Herpetologica 2(2):33–34.
Urosaurus ornatus schmidti Mittleman, 1942, Bull. Mus. Comp. Zool. 91:135–136.

The recognition of this subspecies is based entirely on the specimen (DHD and HMS No. 72) reported by Smith (1935) from 3 mi S of Samalayuca, Chihuahua, and two specimens (UTEP 3362–3) from 7 mi NW of Indian Hot Springs, Texas, presumably across the Río Grande in northern Chihuahua. In our limited collecting south of Ciudad Juárez to Villa Ahumada we did not see a *Urosaurus*. Both UTEP specimens are females with the following characters: ventrals 64, 64; femoral pores 13–13 in both and with S-V length 41 and 48.2 mm, respectively. The color is light gray to cream on both the dorsal and ventral surfaces, with little spotting dorsally and immaculate ventrally; large preshoulder blotches present in *U. o. caerulea* are represented in *schmidti* only as a small dark spot; enlarged dorsals variable in size but equal or subequal to prefemoral or pretibial scales. Head longer than wide, 9.8 to 8.4 and 9.2 to 7.6 mm, respectively. Enlarged dorsals begin at shoulders and extend to base of tail.

Urosaurus ornatus schottii (Baird)

Uta schottii Baird, 1858, Proc. Acad. Nat. Sci. Philadelphia 10:253.
Urosaurus ornatus schottii Mittleman, 1942, Bull. Mus. Comp. Zool. 91:137–139.
Río Bavispe below Tres Ríos near Chihuahua-Sonora state line, 21 (BYU 13427–8, 13430, 13436–8, 13453, 13461, 13466–8, 13471, 13473, 13503, 13507, 13595, 14559–62, 14565–6).

Although there is some doubt as to the exactness of the type locality, if we assume, as have others (Mittleman 1942, Smith and Taylor 1950), that it is in north and central Sonora, then the vicinity of Magdalena may represent the most logical area. Past studies of this species in Sonora (Mittleman 1942, Oliver 1943, Smith and Taylor 1950) have not agreed as to which subspecies of *ornata* occur in Sonora or Chihuahua nor as to their present distribution. Bogert and Oliver (1945) list *U. o. lateralis* for the entire state of Sonora. Smith and Taylor (1950) do the same for *U. o. schottii* and exclude *lateralis*. It may be that both occur, one in the north (*schottii*) and one in the south (*lateralis*), with the latter extending into Sinaloa (see Hardy and McDiarmid 1969).

In attempting to allocate the Río Bavispe specimens, we compared them with a few specimens from the following localities in Sonora: 12 mi NW Altar, Kino Bay, 23 mi N Kino Bay, 10 mi N Guaymas and Ortiz.

Although there is variation in these and the Río Bavispe series, all were well within the basic characteristics, as I understand them, for *U. o. schottii*. The following characters were noted: two rows of enlarged dorsals commencing on the nape and separated by a series of small middorsal scales. Each row of enlarged dorsals consists of two rows of enlarged scales of equal or subequal size. In most specimens the outer rows were smaller but this was not a consistent character.

In most specimens (80%) the enlarged dorsal scales extend onto the posterior part of the nape. In this there is variation ranging from the angle of the shoulder to approximately halfway to the parietal area. The small mid-dorsal scales are irregular in size and are usually two (not more than three) in number across the median. They extend beyond the base of the tail for 3 to 10 of the enlarged dorsal tail scales.

Males have blue belly patches, which in some are divided medially by a light stripe. Most adults are a solid blue from axilla to groin, with little or no blue between the front and hind legs. Females possess faint blue ventral patches or are without them.

Gulars are faint blue in the middle only, not extending to labials. The area of the gular fold is spotted and without blue. This is in contrast to *caeruleus*. Scales on the forearm are equal to but usually not larger than those of enlarged dorsals.

Usually a distinct dark collar extends from in front of the shoulder to or nearly to the enlarged dorsals. A series of 4 or 5 dark, irregular blotches occur from nape to base of tail and usually involve the dorsolateral row of enlarged tubercles. This pattern is in contrast to 6–7 blotches in *caeruleus*.

The measurement ratios of head width to length were too variable to be useful. The head length average for 20 Río Bavispe specimens is 9.5 and width 8.6; two of the 20 had heads wider than long (9.4 - 9.9 and 8.5 - 9.1). In others the length was 0.5 to 1.0 mm longer than wide. The S-V measures were 41–49 mm in the Río Bavispe series and for northern and western Sonora 40–50 mm.

Specimens of *U. ornata* are not available from southwestern Chihuahua. Yet, there is every reason to suspect their presence in the lower Urique basin north of Choix, Sinaloa. The subspecies *U. o. lateralis* would be expected to occur since it is in southeastern Sonora and northeastern Sinaloa. A specimen (BYU 36824) from 15 km ENE of Navojoa, Sonora, has the basic characteristics as presented by Oliver (1943), only one row of enlarged dorsals on each side of the small mid-dorsals; enlarged dorsals extending nearly to parietals; scales on forearm smaller than enlarged dorsals. It is an adult male and quite distinct from the more northern specimens of *ornata*.

Urosaurus bicarinatus tuberculatus (Schmidt)

Uta tuberculatus Schmidt, 1921, Amer. Mus. Nov. 22:4.
Urosaurus bicarinatus tuberculatus Mittleman, 1942, Bull. Mus. Comp. Zool. 91:169–170.
Urique, 1 (BYU 14321).
Near Pitahaya, 1 (BYU 22681).

Two other specimens have been examined: KU 47401 from La Bufa and USNM 14248 from Batopilas. The latter is the type of *Urosaurus unicus* Mittleman and was compared to the Chihuahua specimen from Urique and nearby Sinaloa specimens by Tanner and Robison (1959). Oliver (1943) questioned the validity of *U. unicus*, and Hardy and McDiarmid (1969) agreed that it was at best a variant of *U. b. tuberculatus*. My examination of the *unicus* type provided no characters that were not well within the variable parameters of the subspecies *U. b. tuberculatus*.

The extent of the distribution of *tuberculatus* in Chihuahua is as yet unknown. It does occur in the lower portions of Río Urique and Río San Miguel.

Genus *Uta*

Uta stansburiana stejnegeri Schmidt

Uta stansburiana stejnegeri Schmidt, 1921, Amer. Mus. Nov. 15:1–2.
36 mi S Ciudad Juárez, 1 (BYU 15192).
6 mi N Chihuahua City, 1 (BYU 15815).

In all of our collecting we did not find this species to be common in Chihuahua. Between Silver City and Deming, New Mexico, utas were seen regularly, but they seem to be replaced in the desert flats of northern and céntral Chihuahua by the earless lizard *Holbrookia maculata*. In spite of extensive collecting in the greater Casas Grandes area, we did not see a *Uta*, although *Holbrookia* was abundant.

There is reason to believe that the distribution of *Uta* is primarily in eastern Chihuahua, that is, east of Highway 45 and extending east into Coahuila and south through the more desert areas to eastern Durango. The scarcity of utas from Chihuahua is also suggested by Ballinger and Tinkle (1972), who did not list a single specimen from the state (see Ballinger and Tinkle, Fig. 1 and p. 40, material examined), and yet their distribution map (Fig. 5) includes most of Chihuahua. Smith, Williams, and Moll (1963) list 37 specimens taken along the Río Conchos between Julimes and northeast to Alamo. Smith and Taylor (1950) list a single locality, 15 mi S of Ciudad Juárez. The distribution of this species in Chihuahua and its distributional relationship to *Holbrookia maculata* are yet to be determined.

Family Scincidae

Genus *Eumeces*

Smith and Taylor (1950:219) list four species of *Eumeces* as occurring in the Mexican state of Chihuahua (*callicephalus*, *multivirgatus*, *obsoletus*, and *parviauriculatus*). Zweifel (1954) included *brevirostris* and Anderson (1962) added *brevilineatus*. Tanner (1957) examined the USNM 30833 specimen, which was listed by Smith and Taylor (1950) as a questionable representative of the species *multivirgatus*, and, with this one and two additional specimens, named the Chihuahua specimens *E. multilineatus*. A collection of skinks from Durango and Chihuahua examined by Tanner (1958) resulted in the description of *E. brevirostris bilineatus*.

The occurrence of the species *lynxe* in the western mountains of Durango and *humilis* and *parvulus* in the eastern foothills of Sinaloa suggests, on the basis of the many species that have recently been taken in similar habitats in southwestern Chihuahua, that additional species may occur in the state when adequate collecting is done in the rough terrain of southern Chihuahua. My experience indicates that skinks tend to be gregarious. In two similar and nearby habitats, one may have skinks and the other may not. Thus, collecting must be intense and complete. This type of collecting is far from true for much of southwestern Chihuahua and apparently also for the rugged mountains and foothills of eastern Sinaloa and northern Durango.

Eumeces tetragrammus brevilineatus (Cope)

Eumeces tetragrammus brevilineatus (Cope), 1880, U.S. Nat. Mus. Bull. 17:18–19, 44, 46; Taylor, 1935, Univ. Kansas Sci. Bull. 23:283–290; Anderson, 1962, Herpetologica 18(1):56–57; Lieb, 1985, Contributions in Sci., Nat. Hist. Mus. Los Angeles County 357:1–19.

5 mi N Cerro Campana, Sierra del Nido, 2 (MVZ 70702–3).

Lieb (1985) lists specimens for: Santa Clara Canyon, 4.5 mi E Mx Highway 45 (LACM 11640), Sierra del Nido, 4.7 mi W Encinillas (UTEP 62). Anderson (1962) reported that this range extends into the Sierra del Nido of Chihuahua. Although this species may not have been expected by Anderson, its occurrence is not a complete surprise considering the pockets of other species now known to have extended their distribution from the north and east into Chihuahua. The presence of *Phrynosoma douglassii*, *Thamnophis elegans*, *Thamnophis sirtalis*, and *Opheodrys vernalis* are examples of species whose distribution apparently was present in this area before, during, or immediately after the recent ice age. The following desiccation resulted in dispersing those species requiring a more mesic habitat from the low desert valleys into the foothill and mountain habitats. Disjunct distribution and isolated pockets have resulted. A careful examination of the above species would show, as has *Opheodrys vernalis*, the disruption of a once widespread and certainly a more uniform distribution than is presently known (Conant 1974).

Eumeces callicephalus (Bocourt)

Eumeces callicephalus (Bocourt), 1879, Miss. Sci. Mexique et Centr. Amer. 6:431–433; Taylor, 1935, Univ. Kansas Sci. Bull. 23:290–298.

Eumeces tetragrammus callicephalus Lieb, 1985, Contributions in Sci., Nat. Hist. Mus. Los Angeles County 357:1–19.

Río Bavispe at or near Chihuahua-Sonora line below Tres Ríos, 7 (BYU 13145–50 and 14233).

2 mi E Cerocahui, 3 (BYU 14248–50).

Cuiteco, approx. 1 mi NW in steep rocky canyon, 11 (BYU 14259–61, 14608–14615).

3 mi W of Carmen Bridge (across Río Urique), 1 (BYU 22689).

Along trail just west of canyon rim west of Urique, 1 (BYU 14338).

Taylor (1935) lists one from Madera (MCZ).

Lieb (1985) lists the following additional specimens: Guasaremos (MCZ 43389–90), 8 mi W Matachic (AMNH 68295), Pacheco (MVZ 46672), and 3 mi NE Temoris (KU 51462).

Because *Eumeces callicephalus* exhibits several distinct characteristics, it is deemed justifiable to retain it as a species rather than a subspecies of the *tetragrammus* group. It is understood that a close relationship exists between *callicephalus* and *brevilineatus-tetragrammus;* however, they both seem to be evolving with several distinct characters. Salient characteristics of *callicephalus* reported by Lieb (1985) include: a divided postmental scale, postnasal scale present on one or both sides, one or both primary temporals contact parietal, a single postlabial on one or both sides, interparietal enclosed by parietals and a wide separation in distribution (Lieb 1985, Fig. 4). *Eumeces callicephalus* has its entire distribution west of the Continental Divide, whereas *brevilineatus-tetragrammus* group is primarily found in the Sierra Madre Oriental of Mexico, southwestern Texas, and the desert ranges extending west to the isolated population in the Sierra del Nido of Chihuahua.

The distribution of *E. callicephalus* is difficult to explain. All specimens so far collected were taken west of the Continental Divide (except the specimen taken at Pacheco (Lieb 1985), and yet the habitat on the east side in some areas appears ideal. Why the east slopes of the mountains are not occupied is an enigma. If *brevilineatus* is established in the Sierra del Nido, why not in the Sierra Madre, a relatively short distance to the west when compared to the much greater distance to suitable habitat in Coahuila to the east?

The terrain extending west from the Sierra del Nido consists of low mountain ranges which interconnect and provide, in my opinion, a suitable distribution lane for either species. The fact that neither apparently did suggests that these populations, even though closely related, have been separated for a long time and, since both have continued to occupy similar habitats, have retained relating characters. Our attempt to understand the morphological and distributional changes that have occurred and may yet be occurring in the species of this area as a result of the desiccation following the recent ice age is still a major challenge.

The elevational distribution of *callicephalus* may range to at least 2,000 m. The specimen taken just west of the rim above Urique was at about 7,500–8,000 feet in a habitat of oak-madroño-pine with open spaces of rocky outcroppings. Lieb (1985) lists the range to be 900–1,700 m. We found this species to inhabit the canyon of the Río Bavispe and its tributaries (Nutria Creek) of western Chihuahua and eastern Sonora. It did not occur in the higher elevations north of the Río Papigochic where we found *E. multilineatus*. South of the Papigochic and west of San Juanito (Maguarichic and Mojarachic) in the higher elevations, *E. brevirostris* and *E. parviauriculatus* occur. It is south of Creel on the west rim of the Río Urique that we found *callicephalus* in areas at or above 1,700 m. Lieb (1985:8) indicates by map that *E. callicephalus* is found in the mountainous headwaters of the Río Oteros. As noted above, we found only *E. brevirostris* and *E. parviauriculatus*, and suspect *E. callicephalus* to be at lower elevations near the Sonora border.

Table 3. The percentages and frequencies of the following characteristics as observed in 25 specimens of *Eumeces t. callicephalus* from western Chihuahua, Mexico.

Characteristics	Percent/number
Postmental divided	100/25
Postnasals present	75/19
Interparietal enclosed	80/20
Primary temporal contacts parietal one or both sides	40/10
Postlabials single one or both sides	100/25
Nuchal Y-mark present	100/25
Scale rows 28	56/14
Scale rows 26	44/11
Dorsal scales parietals to base of tail	54–60 (56.25)

During 13–18 July 1958, 10 hatchlings, 8 at Cuiteco, 1 east of Cerocahui, and 1 near the west rim of Urique Canyon, were collected. Those west of Cuiteco were recently hatched. A nest of four young, still with the female, were taken from a nest between two large rocks. This nest was on the northeast side of the canyon and in partial shade for part of the day. Four young of another nest were found under a rock about six feet away, but in the same rocky area. They measured 22.8–25.4 mm snout to vent. Those hatchlings taken east of Cerocahui and on the canyon rim were also of this same size. On 26 September 1963 a juvenile was taken below the Carmen bridge near the Río Urique (BYU 22689). It measured 38.0 mm snout to vent.

An analysis of the characteristics of the 25 specimens collected in Chihuahua is summarized in Table 3. Several characters in this series are not consistent with previous studies (Taylor 1935, Lieb 1985). The most notable variation is that of the contact between the primary temporal and the parietal, in which only 40% are sutured. There is a reduction in the percentage of individuals having 28 scale rows around the body. Two adult females each have 26 rows; of the 8 hatchlings collected with them, 3 have 28 and 5 have 26 rows. In the other 15 specimens, only 3 have 26 rows.

I could not discern more than one postlabial, although there are small scales near and above its posterior end and near the ear openings. The postnasals vary in size, which suggests that they represent a portion of the posterior part of the nasal. The size of the anterior loreal does not seem to vary when postnasals are present, but the posterior part of the nasal is noticeably reduced in size when a postnasal is present. The three characters most typical and consistent in the Chihuahua series are: (a) a divided postmental, (b) a nuchal Y-mark, and (c) complete lateral and dorsolateral light stripes.

Eumeces obsoletus (Baird & Girard)

Plestiodon obsoletum Baird and Girard, 1852a, Proc. Acad. Nat. Sci. Philadelphia 6:129 (type locality, Valley of the Río San Pedro, tributary of the Río Grande del Norte, Texas).

Eumeces obsoletus: Cope, 1875, Bull. U.S. Nat. Mus. 1:45.

Taylor (1935) lists a specimen (USNM 1) for the "City of Chihuahua." Whether this refers to Chihuahua City is not clear. We spent considerable time collecting in the vicinity of Chihuahua City and west to Cuauhtémoc, also in the grassy foothills between Casas Grandes and Colonia Juárez without seeing this species. At the present writing, I am aware of only one other specimen collected in Chihuahua, reported by Legler and Webb (1960) from Guadalupe Victoria (approx. 50 mi SE of Chihuahua City), KU 44261. In view of the record reported above and since they do occur in the Big Bend area of southwestern Texas and in southern New Mexico, their range in Chihuahua may include suitable habitat in the desert areas of eastern Chihuahua.

Eumeces multilineatus Tanner

Eumeces multilineatus Tanner, 1957, Great Basin Nat. 17:111–117.

Eumeces multivirgatus mexicanus: Anderson and Wilhoft, 1959:57.

Eumeces multilineatus: Legler and Webb, 1960:18.

García, 1 (BYU 11984).
3 mi N Chuhuichupa, 8 (BYU 13798, 14226–14232).
Yaguirachic, 11 (MVZ 66056–66065).
15 mi S 5 mi E Creel, 1 (KU 44261).
Chihuahua (no locality), 1 (USNM 30833).

The distribution of *E. multilineatus* is at present confined to the higher mountains north and south of the Río Papigochic. I am not familiar with the habitat at Yaguirachic, but from the description of Anderson and Wilhoft (1959), it seems similar to that at García as described in the field notes of Dr. D Elden Beck (1931). Those taken north of Chuhuichupa were on the brow of a steep, rocky slope above the river and just below a grove of pine. We collected seven on 4 July 1958 from the same area, all from under rocks rather than fallen logs near a meadow as reported by Anderson and Wilhoft (1959).

Legler and Webb (1960) reported a specimen taken 15 mi S and 6 mi E Creel (7,300 feet) but did not indicate the type of habitat. The area south of Creel ranges in elevation between 7,000 and 8,000 feet and is habitat comparable to areas north of the Río Papigochic.

The original description of *Eumeces multilineatus* was prepared from two authentic specimens, one from Chuhuichupa and one from García, plus a faded specimen USNM 30833. Since this description, two additional populations have been added to the distribution of the species, one from Yaguirachic and one from SE of Creel. Although there is little, if any, variation in the color pattern of the populations, there does appear to be variation in some of the scale patterns, particularly in the number of scale rows and dorsals. The eight specimens from Chuhuichupa are uniform in having 24 scale rows around the midbody, those from Yaguirachic are 24 except for one with 25, and the one from south of Creel has 25. The dorsals vary from 52 to 59 (55.5).

The supralabials are consistently 7–7, as are the infralabials at 6–6. There are no postnasals, and in none of the specimens listed above is the interparietal enclosed posteriorly by the parietals. The nuchals are 2–2. Perhaps the most noticeable characteristic in the three populations is the uniformity of the color pattern. The consistency of most of the above scale characters and the uniform color

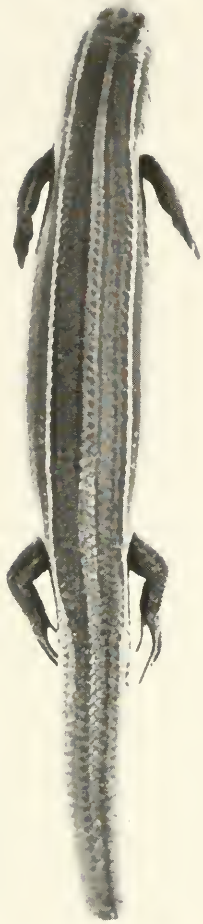

Fig. 7. Dorsal view of the type of *Eumeces multilineatus* (BYU 13798) from 3 mi N Chuhuichupa, Chihuahua.

pattern in contrast to *multivirgatus* are perhaps some of the most significant factors in the establishment of *multilineatus* as a valid species (Fig. 7).

Eumeces multivirgatus Hallowell

Eumeces multivirgatum Hallowell, 1857. Proc. Acad. Nat. Sci. Philadelphia 9:215.
Eumeces multivirgatus mexicanus: Anderson and Wilhoft 1959:57.
Eumeces multivirgatus: Legler and Webb 1960:18.
23 mi S 1.5 mi E Creel, 1 (KU 44260).

Legler and Webb (1960) reported a juvenile specimen taken 23 mi S and 1.5 mi E of Creel. My examination reveals the following characters: 26 scale rows at midbody, 56 dorsals, 1–1 postnasals, 2–3 nuchals, interparietal enclosed by enlarged parietals, a small scale separating postlabial from ear lobules, and a color pattern quite unlike any *E. multilineatus*, but similar in basic pattern to *multivirgatus* seen from Arizona, New Mexico, and Utah.

The color pattern as observed and described by Legler and Webb (1960) implies a relationship to the variations known to occur in *multivirgatus*. In none of the 20 specimens of *multilineatus* examined by me do such color pattern variations occur, but rather a consistently uniform series of scale and color patterns. The following characters are distinctly different from those seen in *multilineatus* and similar to those commonly observed in *multivirgatus:* postnasals usually present, 56–61 rows of dorsals (specimens from Arizona, Colorado, and Utah), interparietal often enclosed posteriorly by parietals, 1 or 2 small scales between postlabials and ear lobules, and a faded variable color pattern.

The Legler and Webb specimen is a recent hatchling and may not exhibit the adult color pattern. In *multilineatus* the color pattern does not seem to vary from hatchling to adult. The scale and color pattern characters do relate this specimen to *multivirgatus*. At present its precise taxonomic status must await additional specimens.

Eumeces parviauriculatus Taylor

Eumeces parviauriculatus Taylor, 1933, Proc. Biol. Soc. Washington 46:178–81; Robinson 1979, Contributions in Sci., Nat. Hist. Mus. Los Angeles County 319:7–9.
2 mi N Maguarichic, 4 (BYU 16849–52).

Robinson (1979) provides a distribution map and reports the following collection localities for this species: 4.8 km NE Temoris (KU 51463–64); La Pulvosa (UMMZ 114502); Mojarachic (FMNH 106476).

Taylor (1933) described this species from a single specimen (USNM 56903) and reported with Knobloch (1940) two additional specimens (KU 18983–4) from the Sierra Madre of Chihuahua. A definite locality was not listed, but I was advised by Dr. Knobloch that these specimens were collected in the vicinity of Mojarachic.

Six of the seven known specimens were found in mountains near the headwaters of the Río Oteros at an elevation above 8,000 feet. This may bring into question the type locality at Alamos, Sonora. Since Goldman undoubtedly collected the other reported species while traveling and then reported from a base camp, it is not likely that Alamos, at 1,200 feet, is the type locality. Goldman (1951) visited the Sierra de Choix (a southwest descending range of the Sierra Madre) northeast of Alamos at elevations of 5,000–6,000 feet. I believe that *E. parviauriculatus* is a mountain inhabitant and is not to be found in the low coastal or foothill valleys much below 5,000 feet. This distribution is also suggested by Robinson (1979). The Maguarichic specimens consist of one adult female with a snout-vent length of 53 mm and three hatchlings ranging from 23 to 26 mm. They were collected together on 15 July 1960. All were in a small burrow beneath two rocks on a southwest slope. The habitat consisted of open, rocky spaces between scattered, low-growing oak and other shrubs. To the west and south was the deep barranca of the Río Oteros. This is the third species of which we collected hatchlings during July (*callicephalus*, 13–18 July 1958; *multilineatus*, 4 July 1958 and *parviauriculatus*, 15 July 1950).

Except that the adult is larger, no other characters vary. In fact, all four are essentially duplicates when compared to the description and drawings of the type. The color pattern is basically the same but is not discolored, showing the dorsolateral stripes a light cream to white and extending from snout onto tail. A lateral stripe is present from labials to front leg. The area between the dorsolateral stripes is a mottling of grayish green, contrasting sharply with the dark brown below the dorsolateral stripes. The venter grades from light to dark gray between the legs, and the gulars are a cream color.

Eumeces brevirostris bilineatus Tanner

Eumeces brevirostris bilineatus Tanner, 1958, Great Basin Nat. 18(2):57–62 (type locality, approximately 10 mi SW El Salto, Durango, Mexico); Dixon, 1969, Contributions in Sci., Nat. Hist. Mus. Los Angeles County 168:1–30; Robinson, 1979, Contributions in Sci., Nat. Hist. Mus. Los Angeles County 319:1–13.

1 mi W La Laja (approximately 6 mi SE Mojarachic), 1 (BYU 16853).

Zweifel (1954) reports two hatchlings (7 mi SW Lagunita, MVZ 59138, and 3 mi N Río Verde, MVZ 59139) taken 30 June and 3 July 1953. Dixon (1969) lists the following localities: Mojarachic (UMMZ 117756); 15 mi S, 6 mi E Creel (KU 44262–63); 2 mi W Samachique (KU 47429, 51324–25); 7 mi SE El Vergel (MVZ-1).

The reviews by Dixon (1969) and Robinson (1979) not only provide a summation of the characteristics of this subspecies but also establish relationships that were not possible for lack of specimen material in previous studies (Taylor 1935, Tanner 1958). Furthermore, areas of distribution have been generally established for the subspecies of *E. brevirostris* and those species related to this group.

A review of my field notes indicates that there were few if any differences in the habitats in which the specimens of *E. b. bilineatus* and *E. parviauriculatus* were found. Both were taken in open areas on a southwest slope in rocky terrain and at approximately the same elevation. Robinson (1979:5, Fig. 2) also cited this sympatric distribution. If one accepts as valid the distribution map of *E. callicephalus* (Lieb 1985), then three species (*callicephalus*, *brevirostris*, and *parviauriculatus*) are sympatric in the Maguarichic-Mojarachic region of southwestern Chihuahua (see Lieb 1985).

Family Teidae

Genus *Cnemidophorus*

In Chihuahua, members of this genus are abundant and during the daytime are one of the more conspicuous lizards in the state. Only the genus *Sceloporus* appears to be more widespread and abundant. Within Chihuahua there are seven species of the genus *Cnemidophorus* as listed below. In addition, *C. neomexicanus* may occur in the north central area (Maslin and Secoy 1986:21), *C. burti stictogrammus* approaches or enters Chihuahua from northeastern Sonora or southeastern Arizona, and *C. g. septemvittatus* is reported for the northeastern corner (Duellman and Zweifel 1962, Maslin and Secoy 1986). Axtell (1961) reviewed the status of *C. inornatus* and described the population in northwestern Coahuila and northeastern Chihuahua as a new subspecies, *C. i. heptagrammus*.

The synonymies of the various species and subspecies reported for Chihuahua are long and have been a source of confusion for many years. During two decades (1950 to 1970) much of the taxonomic confusion that previously clouded our understanding of the systematic and taxonomic relationship of the species of *Cnemidophorus* in northern Chihuahua and the adjoining states has been largely resolved. Only a better understanding of distribution, life history, and ecological relationships apparently remains.

The discovery of all-female species in the areas of south central United States (primarily Arizona, New Mexico, and Texas) and north central Mexico (Sonora, Chihuahua, and Coahuila) led to an intensive study of the genus in the above and adjoining areas (Lowe and Zweifel 1952, Lowe 1956, Maslin, Beidleman, and Lowe 1958, Maslin 1962, Smith, Williams, and Moll 1963, Zweifel 1965, Wright and Lowe 1965, Axtell 1966, Lowe and Wright 1966, Wright and Lowe 1967, Williams 1968, Walker 1981, and others). At present, three parthenogenetic species are known to occur in northern Chihuahua (*exsanguis*, *uniparens*, and *tesselatus*) and perhaps a fourth if the range of *neomexicanus* extends across the border from New Mexico as indicated by Maslin and Secoy (1986). Vance (1978) also plots (map, Fig. 6) *neomexicanus* reaching to the northern border of Chihuahua.

It is now obvious that the phenotypic characters were not adequate to provide a complete understanding of the systematics of the various sympatric populations. The studies of Lowe and Wright, particularly their "Evolution of Parthenogenetic Species of *Cnemidophorus*—1966," brought into focus the genetic foundations which served to clarify the parental background of the unisexual species. A better understanding of this genus in Chihuahua must wait for an in-depth investigation of its species, particularly in the central and northern areas of the state.

In recent studies by Cole (1985), Walker (1986), and others cited by them, the taxonomic problems associated with the unisexual (parthenogenetic) entities in the genus *Cnemidophorus* are discussed. Inasmuch as there are basic unresolved judgments concerning the proper system of names to be applied to these populations, I have retained them as species, recognizing their yet undetermined taxonomic status. In this study their distribution in Chihuahua is the main reason for citing them.

The recent publication "A Checklist of the Lizard Genus *Cnemidophorus* (Teidae)," by the late T. Paul Maslin and Diane M. Secoy (1986), provides a complete listing of the species and subspecies of the genus as well as synonymies, holotype and type localities, general range designations, and useful remarks. This study will undoubtedly serve as a starting point for future studies of this widespread and diverse American genus.

Cnemidophorus costatus barrancorum Zweifel

Cnemidophorus costatus barrancorum Zweifel, 1959, Bull. Amer. Mus. Nat. Hist. 117:57–116; Duellman and Zweifel, 1962, Bull. Amer. Mus. Nat. Hist. 123:157–210.

Urique, 6 (BYU 14326, 14328–32).

10 mi below (SW) Guachochic, 1 (BYU 22674).

The Chihuahua population appears to have fewer granules at midbody than the average given by Duellman and Zweifel (1962) at 103.1. None of the Chihuahua specimens approach 100. Otherwise there are few differences.

The distribution must yet be determined. At present it occurs in both the Río San Miguel and Río Urique basins and undoubtedly is in the lower Oteros basin.

Cnemidophorus exsanguis Lowe

Cnemidophorus exsanguis Lowe, 1956, Bull. Chicago Acad. Sci. 10:137–150.

Colonia Dublán, 3 (BYU 11962–3, 17100).

2 mi N Colonia Juárez (Tinaja Wash), 2 (BYU 13353–4).

Near Red Rock (Tinaja Canyon), 4 (BYU 15458–60, 17044).

3 mi W Colonia Juárez, 10 (BYU 13417–26).

Río Bavispe, below Tres Ríos near Chihuahua-Sonora line, 15 (BYU 13364–66, 13444, 13460, 13462, 13468, 13472, 13474, 13504, 13590–1, 13594, 14558).

Los Chales, 24 mi NE Tres Ríos, 1 (BYU 15826).

18.5 mi E Ricardo Flores Magón, 6 (BYU 13399–400, 13406–9).

5 mi E Colonia Dublán, 6 (BYU 14158–61, 14648, 13476).

Pacheco, 1 (BYU 14146).

60 mi S Sueco near El Saúz, 5 (BYU 14156, 15300, 15307, 15309, 15348).

Call Canyon, near Colonia Juárez, 4 (BYU 41756–9).

Temosachic, 10 (UTEP 2054 [4 specimens], 2058, 2251–4, 2258).

4.1 mi ENE Buenaventura, 1 (UTEP 3571).

Duellman and Zweifel (1962) list the following additional localities: Lake Santa María, 30 mi W Casas Grandes near Cuerba, Río Gavilán, 7 mi SW Pacheco, Ramos, Río Papigochic near Ciudad Guerrero, 37 mi S 3 mi W Ciudad Juárez, 4 mi S 1 mi E Moctezuma, 20 mi S Gallegos, 7.5 mi S Gallegos, and 10 mi W Namiquipa (19 specimens).

Smith, Williams, and Moll (1963) list 15 specimens from Julimes and 2 mi N of Julimes. These records, and the list above, indicate that the distribution of this species in Chihuahua extends at least south to near Delicias and northwest through the low ranges to the Río Papigochic. We did not collect it in the basin of Chihuahua City where *C. scalaris* was collected.

Those populations in central Chihuahua (west of Highway 45 and east of the mountains) are apparently a southern extension of those in New Mexico. That is, the color pattern and scalation are essentially the same, with six light longitudinal stripes, 67–79 (72.4) scale rows around midbody, and 4–7 scales between the paravertebral light stripes at or near midbody (based on 18 specimens).

A series of 15 specimens from the Río Bavispe are similar in color pattern but variable in scalation. Scale rows around midbody range from 70 to 85 (76.9), and the scales between the paravertebral stripes are 5–7. The largest specimen measured 85 mm in snout-vent length, and several hatchlings collected in late August were 31.5–38.6 mm in snout-vent length.

Cnemidophorus gularis scalaris Cope

Cnemidophorus gularis scalaris Cope, 1892, Trans. Amer. Philos. Soc. 17:47; Maslin and Secoy, 1986, Contributions in Zool., Univ. Colorado Mus. 1:16.
6.4 mi N 1.5 mi W Chihuahua City, 5 (BYU 15375, 16978–9, 17008–9).
48 mi W Chihuahua City (along Highway 16), 1 (BYU 13908).
27 mi S Parral, 4 (BYU 15653–6).
15.4 mi S Villa Matamoros, 4 (BYU 41773–6).
9 mi N El Saúz Junction, 1 (UTEP 1320).
1 mi S Camargo, 1 (UTEP 1321).

Duellman and Zweifel (1962) list 56 specimens from 17 mi N of Chihuahua City and south to near Durango; Smith, Williams, and Moll (1963) list two specimens from La Boquilla. The most northern locality appears to be 9 mi N of El Saúz Junction.

The maximum snout-vent length is 101 mm (BYU 15375), which is larger than that reported by Duellman and Zweifel (1962). Granules around midbody 75–91 (82.5); ventrals, from gular fold to anus, 39–43 (40.5); femoral pores (total) 32–38 (34.4), and 3–9 scales separating the paravertebral stripes. In two hatchlings (BYU 15656 and 41775) the scales between the paravertebral stripes are less variable (6–9 at or near midbody) since the stripes are straight, whereas in adults these stripes become irregular, producing considerable variation in the number of scales between them.

In contrast to the six specimens from Chihuahua City environs reported by Duellman and Zweifel (1962:198), five specimens from just north of the city have 77–90 (83.8) granules at midbody as opposed to their reported 82–92 (86.5). Specimens taken from the same collecting area may vary as much as 10–15 granules and may account for some of the systematic divergence occurring in recent studies dealing with the nomenclature of this and other species of *Cnemidophorus*.

Cnemidophorus inornatus heptagrammus Axtell

Cnemidophorus inornatus heptagrammus Axtell, 1961, Copeia 1961(2):148–158.
2 mi N Gallego, 9 (UTEP 3496–3502, 3512–13).

Axtell described the west central (western Coahuila and eastern Chihuahua) populations as *C. i. heptagrammus*. Wright and Lowe (1965) redescribed *C. i. arizonae* in eastern Arizona, and Williams (1968) described as new the southern populations (Durango and northern Zacatecas) as *C. i. paululus*. The distribution of *C. i. heptagrammus* in Chihuahua is not as yet fully determined. Present records are from an area west from Coahuila to or near Highway 45 and south of Ciudad Juárez along the highway to El Saúz. I have no records for northwestern Chihuahua where *inornatus* may occur either as the subspecies *heptagrammus* or *arizonae*.

Those Chihuahua specimens I have seen have GAB 58–62, ventrals 37–39, femoral pores (total) 32–35, and 7 complete body stripes in all but one, in which the median is only a faint, incomplete stripe for a short distance posterior to the parietal. Other characters are within the parameters set forth in the original description.

Cnemidophorus uniparens Wright & Lowe

Cnemidophorus uniparens Wright and Lowe, 1965, Jour. Arizona Acad. Sci. 3(3):164–68.

6.1 mi (by road) NE Janos, 1 (UTEP 3570).
14.7 mi (by road) SW Ricardo Flores Magón, 1 (UTEP 3572).
19.3 mi (by road) ESE Ricardo Flores Magón, 4 (UTEP 3573–76).
6.2 mi (by road) W El Sueco, 2 (UTEP 3577–8).

It appears that *C. uniparens* may be sympatric with *C. exsanguis* in local areas. The distribution of the species in northern Chihuahua will need a careful study before an understanding of the distribution of the unisexual species of northern Chihuahua is achieved.

Cnemidophorus marmoratus marmoratus Baird & Girard

Cnemidophorus marmoratus Baird and Girard, 1852a, Proc. Acad. Nat. Sci. Philadelphia, p. 128.
Cnemidophorus tigris marmoratus: Burger, 1950, Chicago Acad. Sci. Nat. Hist. Misc. 65:7.
Cnemidophorus marmoratus marmoratus Hendricks and Dixon, 1986, Texas J. Sci. 38(4):327–402.
21.5 mi N Ascensión, 1 (BYU 14508).
30 mi (by road) S Ciudad Juárez, 1 (BYU 15208).
36 mi (by road) S Ciudad Juárez, 3 (BYU 15204–6).
.5 mi S Las Palomas, 2 (UTEP 3410–11).
4.7 mi S Samalayuca, 2 (UTEP 3472–3).
24 mi NNE Ascensión, 1 (UTEP 3567).

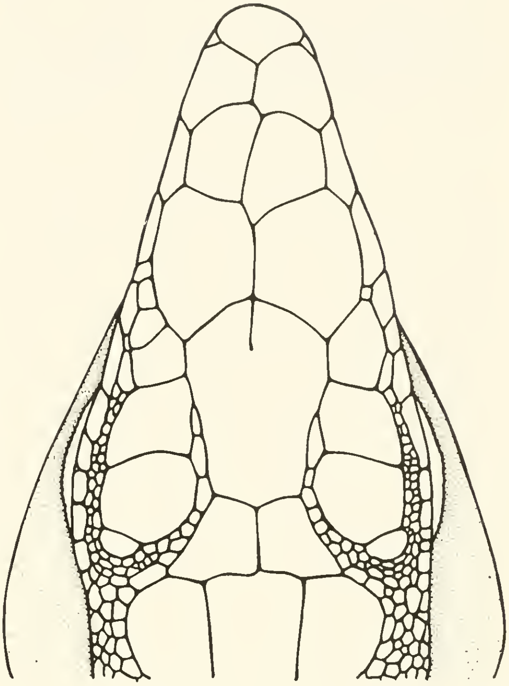
Fig. 8. Dorsal head scales of *Cnemidophorus tigris marmoratus* (BYU 14508) from 21.5 mi N Ascensión, Chihuahua.

Burger (1950) diagnosed *marmoratus* by color pattern and superciliary granules as follows: dorsal color pattern a reticulum of several broken light stripes usually evident middorsally and with vertical bars frequently accentuated on the sides; chin white or graying with black spots; belly white, checkered anteriorly with gray and black. The superciliary granules may extend to the first supraocular (Fig. 8). Zweifel (1959) added the following scale patterns for two series of specimens: granules around body, 26 specimens from Coahuila, 87–110 ($\bar{x}$ = 100.2), and for Alamogordo, New Mexico, 15 specimens, 91–116 ($\bar{x}$ = 102.5). Six specimens from Chihuahua have 88–108 ($\bar{x}$ = 97.8). For the same populations the femoral pores are as follows: 38–48 ($\bar{x}$ = 43.6), 40–48 ($\bar{x}$ = 45.3), and those from Chihuahua 41–46 ($\bar{x}$ = 44.0).

The color pattern in adults is not a clearly defined striped pattern and may exhibit a variation of broken stripes to irregular undulating spots on the body. At or near the nape, and extending from the head, stripes may be discerned for a short distance.

I have made no attempt to define the differences in either the color or scale patterns between the two sympatric species, *C. marmoratus* (and *C. tigris*) and *C. tesselatus*. However, it is obvious that there is a great similarity which perhaps misled Burt (1931), and thus his *C. tesselatus* included a composite. An understanding of this complex was not fully resolved until the distinction of unisexual and bisexual species was established (Zweifel 1965).

Cnemidophorus marmoratus reticuloriens Hendricks & Dixon

Cnemidophorus tigris pulcher Williams, Smith, and Chrapliwy 1960, Trans. Illinois Acad. Sci. 53:43–45.
Cnemidophorus marmoratus reticuloriens Hendricks and Dixon, 1986, Texas J. Sci. 38(4):327–402.
33 mi (by road) S Chihuahua City, 1 (BYU 15812).

The above specimen is included by Hendricks and Dixon (1986) in the series with the subspecies *reticuloriens*, and yet it has a color pattern that approaches *C. m. pulcher*. The throat and chest are heavily pigmented and the venter is a dark brown. The gulars, though sooty brown, do have large dark spots unlike those in more northern *marmoratus*. The dorsal and lateral body pattern is without recognizable stripes and consists of dark to light brown reticulations. A series of dark vertical bars extend from the enlarged ventrals dorsad to the dorsal reticulations, a pattern similar to that of *C. m. marmoratus*.

The scale characters are as follows: dorsals 94, GAB 95, femoral pores 20–21 (41) with 3 scales separating them, enlarged ventrals in 8 rows, ventrals 42 from gular fold to preanals, supralabials 5–5, infralabials 6–6, supraoculars 4–5 with posterior scale on left side divided, circumorbitals only to suture of second supraocular, interparietal single and with two rows of enlarged scales posterior to it, no frenocular, two suboculars with the anterior one enlarged, extending anteriorly and curving dorsad to lie below and in front of the eye, dorsals from occiput to base of tail 202.

The distribution of *C. marmoratus* and its subspecies is not as yet fully understood. This single specimen, although placed in the subspecies *reticuloriens*, does not fit well into the description set forth by Hendricks and Dixon (1986). The color pattern is similar to the subspecies *m. pulcher* in that the gulars have large dark spots occupying at least half the gular area, the venter is mostly dark brown, and the dorsum is without recognizable lines.

This specimen (BYU 15812) appears to be an intergrade between *reticuloriens* and *pulcher*, but with strong indications that it is close to the latter. At least the influence of *m. pulcher* seems to extend north of the type locality in southeastern Chihuahua into the desert areas to the north and perhaps into the Balson Mapimi.

Cnemidophorus tesselatus (Say)

Ameiva tesselata Say, 1823, Long Expedition to Rocky Mountains 2:50.

Cnemidophorus tesselatus: Smith and Burger, 1949, Bull. Chicago Acad. Sci. 8:282; Zweifel, 1965, Amer. Mus. Novitates 2235:1–49.

Smith, Williams, and Moll (1963) reported 62 specimens between Julimes and Alamo along the Río Conchos. Specimens from this area were studied by Zweifel (1965) and related to populations in central New Mexico. Zweifel's illustration in Figure 2-E from Socorro County, New Mexico, is very similar in dorsal (and lateral) color pattern to an adult female specimen of *C. m. marmoratus* taken in northern Chihuahua (BYU 14508). In the latter specimen the stripes are interrupted from near the shoulders posteriorly, and the sides of the body have a series of 12–13 vertical bars between the legs. There are 102 granules at midbody; 41 total femoral pores; circumorbital scales reach anterior to half of the second supraocular, a condition equal to class III in Figure 5, p. 17, of Zweifel (1965). In other scale patterns the mesotychials are enlarged but the postantebrachials are only slightly enlarged; fourth supraocular small, with a small scale preceding the first supraocular; S-V length 94.5 mm.

The demonstration that *C. tesselatus* is a unisexual species served to clarify the systematics of a large group within the genus. The fact that *C. tigris* and *C. tesselatus* have individuals, in some populations, with very similar scale and color patterns may have induced Burt (1931) to include the widely dispersed *tigris* as a synonym of *C. tesselatus*. Except for the small dark spots widely dispersed on the venter of female *C. m. marmoratus* from Chihuahua, little color pattern difference seems to exist between these sympatric species.

The distribution in Chihuahua is not known beyond those specimens reported above.

Family Anguidae

Genus *Barisia*

Barisia levicollis Stejneger

Barisia levicollis Stejneger, 1890, Proc. U.S. Nat. Mus. 13(809):184.

Gerrhonotus imbricatus levicollis Dunn, 1936, Proc. Acad. Nat. Sci. Philadelphia 88:368.

Barisia levicollis: Tihen, 1949, Univ. Kansas Sci. Bull. 33(1):2478.

Barisia imbricatus: Guillette and Smith, 1982, Trans. Kansas Acad. Sci. 85(1):13–32.

Chuhuichupa, 1 (BYU 13898).

16 mi NE San Juanito, 1 (BYU 17023).

We did not find *Barisia* to be numerous. Both specimens were found on hillsides in a shrub habitat, and both were moving when first observed. The Chuhuichupa specimen is a female, 145 mm in snout-vent length, with an incomplete tail.

Both specimens were taken in low shrub, brushy habitat and not on rocky hillsides. This type of habitat is not an easy collecting area and may account for the few specimens taken, not only by us, but by others.

The name usage here follows Tihen (1949) and Smith (1986). For additional records see Guillette and Smith (1982).

Genus *Gerrhonotus*

Gerrhonotus kingii kingii (Gray)

Elgaria kingii Gray, 1838, Ann. Mag. Nat. Hist. 1:390.
Elgaria kingii kingii Tihen, 1948, Trans. Kansas Acad. Sci. 51(3):299–301.
Gerrhonotus kingii kingii Webb, 1970, Cat. Amer. Amph. Rept. 97.1.
Río Bavispe below Tres Ríos, near Chihuahua-Sonora line, 1 (BYU 13442).
3 mi N Chuhuichupa, 2 (BYU 13902, 15473).
4 mi N Chuhuichupa, 1 (BYU 15422).

The color pattern would fit either of the northern subspecies, although some variation is present. The transverse rows of dorsal scales number 54–56. A clear-cut definition appears difficult; therefore, I place them in the subspecies *kingii*, but they may, as indicated by Webb (1970), all come from a zone of intergradation.

Gerrhonotus kingii ferrugineus Webb

Gerrhonotus kingii ferrugineus Webb, 1962, Herpetologica 18(2):73–79.
Near Piedras Verdes, 1 (BYU 22676).

The color pattern is as described by Webb (1970): dark cross bars on body with only one row of scales in each bar with distinct dark and light markings. Dorsal head scales uniform brown; tail with 5 dark bars or spots on dorsals, ventral area of body and tail without any dark markings. Dorsal transverse scale rows between the lateral folds 16 with the scales in the lateral rows only half the size of scales in the other rows; ventral rows 12.

This locality is in the drainage of the Río Urique a short distance northwest of its junction with the Río San Miguel. Collecting localities cited by Webb (1970) are north of the Barranca del Cobre some distance from Piedras Verdes. The latter locality is only a short distance from the Chihuahua-Sinaloa line and may represent the most northern limits of *G. k. ferrugineus*. It was taken at an elevation of approximately 6,000 feet.

Gerrhonotus liocephalus taylori Tihen

Gerrhonotus liocephalus taylori Tihen, 1954, Amer. Mus. Novitates Bull. 1687:1–26.
Clarines Mine, 5 mi W Santa Bárbara, 1 (AMNH 67918).
Santa Bárbara, 1 (AMNH 68235).

These specimens collected by G. M. Bradt in 1947 are, to my knowledge, the only ones known from Chihuahua. I have not seen them and can only suggest that the uplands of southern Chihuahua may yet provide new taxa and distribution records when its herpetofauna is fully known.

Acknowledgments

Many individuals and families assisted in the field work conducted in various parts of Chihuahua. We were accepted not only by the American colonists but also by the Mexican and Indian individuals with whom we came in close contact upon several occasions.

In Colonia Juárez we were fortunate in having an opportunity to stay at the homes of Mr. and Mrs. David Johnson, Jr., and Mr. and Mrs. Irvin Romney. The Turleys were also very helpful. Perhaps those most understanding of our aims in the gathering of material were the Hatch brothers, Herman, Roy, and Seville. We were particularly grateful to the Herman Hatch family, who not only permitted us to bed down under the old apple tree at any hour of the day or night, but who also offered us their hospitality and served as information agents for our travels in much of northern and central Chihuahua (Fig. 2).

Our first trip into the mountains was with the Colonia Juárez scout troop to the Río Bavispe (just below Tres Ríos), and the next year with Amilio Borgous to Chuhuichupa. These trips introduced us to the mountains and prepared us, we thought, for the barrancas of southwestern Chihuahua.

In Colonia Dublán, Mr. Alma Jarvis, the postmaster, provided us with valuable information concerning areas for which he was well informed. Mr. and Mrs. Keith Bowman, upon a number of occasions, provided us with meals and a place to stay.

In Ciudad Chihuahua we were fortunate in becoming acquainted with Mr. Harold Pratt, the Chihuahua agent for the Alice-Chalmers Equipment Company. Mr. and Mrs. Pratt opened their home to us, and provided an opportunity for us to rest after having been in the mountains for a time, and also an opportunity to curate and reassemble our collections in preparation for the trip home. It was from their estate that we were able to spend collecting time in the Ciudad Chihuahua area. We were also fortunate to have met a friend, Mr. Ray Thane, in San Francisco del Oro, who provided us with information and an opportu-

nity to visit with a Mexican family.

During the years spent in Mexico I had the good fortune of having as companions a number of capable faculty and graduate students. The first trip (1956) involved Mr. Verle Allman, a biology teacher, and my son Lynn. For the next four years I had as my companion Dr. Gerald W. Robison, now at the Bethesda, Maryland, research center. We were accompanied, upon one occasion (1958), by Dr. and Mrs. Irving W. Knobloch, professor of botany from Michigan State University, and upon another occasion by Dr. Stephen L. Wood, an entomologist from Brigham Young University and his graduate student, Dr. Jay Karren.

The trip to Urique with Dr. Knobloch was a highlight, as was the trip with Dr. Wood to Maguarichic. Each trip added to our species list and seemed to compel us to plan the next trip. In October of 1963 I was a member of the John Cross expedition into the Barranca del Cobre. Although we could not run the river as planned, we did get considerable publicity in both the Chihuahua and U.S. newspapers and had the opportunity to secure additional material and data. Mr. John Cross is an accomplished adventurer and river runner, having been interested in commercial river expeditions during much of his life. His interest in the rivers of southwestern Chihuahua was thus not only a part of his vocation but also an adventure for him into a new river system. Mr. Cross made at least three additional trips into the barrancas of southwest Chihuahua, two down the Río Urique and one from the Río Verde, south of Guachochic, into the Río San Miguel and to the junction of the Río Urique. Although herpetology was not their prime interest, a number of new records for Chihuahua were obtained and the specimens deposited in the BYU collection.

During the next few years I had as my companions either Dr. Glen T. Moore, a botany professor at BYU, or Dr. Kenneth R. Larson, a graduate student at the time.

Upon occasion we solicited the aid of local citizens, particularly when we were shorthanded in the mountain areas. Everyone was helpful and cooperative. This occurred, for example, when we were at Creel. The La Bufa mining superintendent helped us secure the necessary supplies and travel information to complete our trip into the southwestern barranca area.

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DRY-YEAR GRAZING AND NEBRASKA SEDGE (*CAREX NEBRASKENSIS*)

Raymond D. Ratliff[1] and Stanley E. Westfall[1]

ABSTRACT.—In 1984 (a dry year), Tule Meadow, in the Sierra National Forest, California, was well grazed after several years of light use. This situation provided the opportunity to study responses of Nebraska sedge (*Carex nebraskensis*), an important forage species in mountain meadows, to protection and grazing. Rooted shoot frequencies and densities in fall 1984 and spring 1985 were the same within an exclosure and on the grazed area. Residual herbage (shoot weight) in fall and shoot heights in spring were greater within the exclosure. Lower spring shoot heights on the grazed area may relate to fall regrowth and reduced insulation induced by grazing. Nitrogen and potassium content of fall herbage was greater on the grazed area. Phosphorus content was the same both inside and outside the exclosure.

Nebraska sedge (*Carex nebraskensis*) is found from Kansas to California and from New Mexico to Canada (Hermann 1970). It is generally palatable to cattle and horses. A valuable species on many mountain meadows, Nebraska sedge is often grazed heavily during summer. However, at Tule Meadow (Sierra National Forest, California) grazing of Nebraska sedge and the meadow as a whole is largely controlled by weather.

Under average conditions, Tule Meadow has a wet center and relatively dry edges. In wet years only the edges of the meadow receive significant use, although cattle occasionally wade out to graze on preferred parts of specific plant species. In dry years all parts of the meadow receive significant use. From 1979 to 1983 cattle grazed mainly along the edges of Tule Meadow, leaving most of it ungrazed or lightly grazed. Earlier, Pattee (1973) reported that cattle spent 100% of their time on the edges.

Cattle grazing Tule Meadow had made substantial use of Nebraska sedge by mid-July 1984. By the end of August no ungrazed patches of meadow remained (Fig. 1). By October surface water was present only at the lowest point—a very rare occurrence.

At Wishon Dam, a few miles east of Tule Meadow, precipitation in 1984 totaled 76 cm, only 50% of the 1977–1985 average (152 cm). In addition, monthly maximum and mean air temperatures from January through September were higher than the 1977–1985 average.

We took advantage of this extraordinary condition of dryness to ask how grazing in such a year would affect Nebraska sedge. Would shoot frequencies, shoot densities, shoot heights, residual herbage weights, and nutrient contents be the same inside a livestock exclosure and outside where grazing had occurred? Could grazing in a dry year benefit the Nebraska sedge population by stimulating vegetative reproduction?

METHODS AND MATERIALS

STUDY AREA.—Tule Meadow, in the montane zone at an elevation of 2,170 m, is a basin type with vegetated margins (Ratliff 1985). It lies in a swale formed by lateral moraines (Wood 1975) and usually has surface water all year. Beneath the sod an organically rich topsoil extends to depths of 90 to 120 cm. Soil texture ranges from sand to silt loam. Inorganic, gleyed material extends to 275 cm.

In 1979 we established an exclosure in a lotic Nebraska sedge site (Ratliff 1985). Within the exclosure we studied seasonal biomass trends, Nebraska sedge morphology, carbohydrate levels (Steele et al. 1984), and shoot life history (Ratliff 1983). Except for the life history plots, the exclosure has been undisturbed since fall 1981 and has returned to prestudy conditions.

SAMPLING.—We randomly located points on grid systems. Inside the exclosure we located 60 points on a half-meter grid within a 238-m^2 area. In the remainder of the Nebraska sedge site, about 1 ha, we located 120 points on a 1-m grid. Independent sets of grid points were selected for fall (3 October 1984) and

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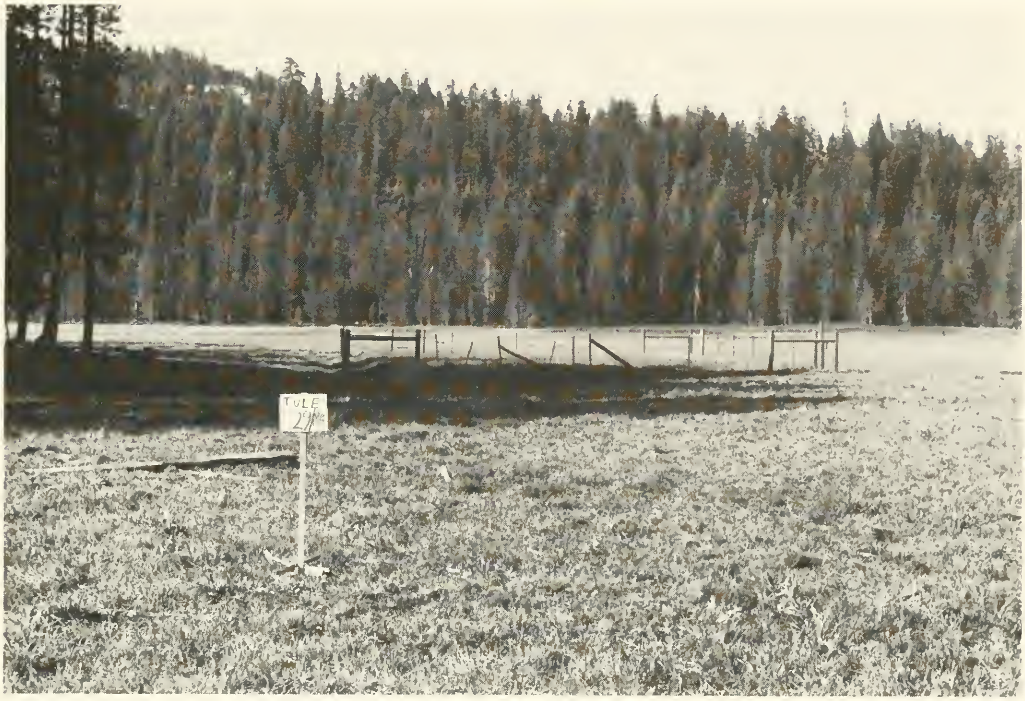

Fig. 1. Tule Meadow, Sierra National Forest, California, showing extent of grazing by cattle in 1984.

spring (16 May 1985) sampling.

Quadrats (10 × 20 cm) were centered at the grid points. Presence or absence of Nebraska sedge shoots in the quadrats was noted. Rooted frequency (% presence) was computed for fall and spring samples. In fall, current mature shoots (vegetative and reproductive) and juvenile shoots (shoots with three or fewer leaves unfolded) of Nebraska sedge were counted to estimate shoot densities. The shoots were then cut off at the surface to estimate residual herbage weights.

The herbage was oven-dried (24 hrs at 60 C) and weighed. Total nitrogen (N), phosphorus (P), and potassium (K) in the shoot material was estimated at a commercial laboratory. Analysis procedures were N—Kjeldahl nitrogen, P—nitric, perchloric acid digestion, and spectrometry, and K—hydrochloric acid digestion and spectrometry. Some grazed quadrats did not contain sufficient Nebraska sedge for the chemical analyses; therefore, materials from up to four randomly selected, grazed quadrats were combined.

In spring, close observation was required to distinguish the previous year's mature vegetative shoots from the rapidly expanding younger shoots. Also, surface water depth precluded efficient cutting of shoots. Therefore, all live shoots of Nebraska sedge rooted in the quadrats were counted, and the height of the tallest one was measured.

STATISTICS.—We took advantage of current conditions of weather and grazing; replication of treatments was not possible. Differences between the exclosure and the grazed area should therefore not be extrapolated to other sites. Nevertheless, the comparisons provide new insight on response of an important meadow species, Nebraska sedge, to grazing.

For each data set we computed the 95% confidence intervals for the means. In the case of frequencies the confidence intervals were for the proportions of quadrats with Nebraska sedge. The hypothesis of no difference between analogous characteristics was rejected when the 95% confidence interval for the difference (grazed area vs. exclosure) covered zero. Standard methods of calculation (Steel and Torrie 1960) were used.

Fall and spring values were not compared since different kinds of data were involved. Also, reproductive shoots included in the fall sample died before spring. Total shoot densi-

TABLE 1. Means and confidence intervals for Nebraska sedge shoot frequency, density, residual herbage weight, height, and nutrient content and differences under grazing and protection at Tule Meadow, Sierra National Forest, California.

	Treatment		Difference
	Grazed	Protected	(G - P)
Measure	$\bar{X} + \text{CI}^a$	$\bar{X} + \text{CI}$	$\bar{d} + \text{CI}^b$
Frequency (%)			
Fall 1984	91 ± 5	82 ± 10	9 ± 11
Spring 1985	91 ± 5	88 ± 8	3 ± 10
Density (shoots/m^2)			
Fall 1984			
Total	380 ± 63	357 ± 76	23 ± 103
Mature	274 ± 46	266 ± 56	8 ± 75
Juvenile	106 ± 22	91 ± 24	15 ± 35
Spring 1985	296 ± 44	231 ± 47	65 ± 69
Weight (g/m^2), fall 1984	62 ± 11	172 ± 43	−111 ± 33
Height (mm), spring 1985	144 ± 7	198 ± 14	−54 ± 13
Nutrients (%), fall 1984			
Crude protein^c	6.31 ± 0.41	5.48 ± 0.28	0.81 ± 0.50
Phosphorus	0.11 ± 0.01	0.11 ± 0.01	0.00 ± 0.01
Potassium	1.33 ± 0.09	1.00 ± 0.04	0.33 ± 0.11

[a] 95% confidence intervals for proportions and means
[b] 95% confidence intervals for differences
[c] Nitrogen (%) × 6.25

ties between fall and spring were therefore expected to be different.

RESULTS AND DISCUSSION

FREQUENCY.—In 1984, grazing did not affect rooted frequencies of Nebraska sedge shoots in the 10 × 20 cm quadrats (Table 1). The differences in proportions of occupied quadrats in the exclosure and in the grazed area in fall and spring were no more than expected by chance. All observations combined, Nebraska sedge frequency was 88.9% ± 3.2%.

Juvenile shoot frequency in the fall was neither enhanced nor reduced by grazing. The frequencies were 67% ± 12% inside and 68% ± 8% outside the exclosure.

DENSITY.—Greater density on the grazed area could occur if grazing stimulated tiller and rhizome production. However, grazing in 1984 did not affect densities of Nebraska sedge shoots (Table 1).

Nevertheless, interpreting the confidence interval, we are 95% confident that the maximum possible differences in fall were −80 shoots per m^2 (23 − 103) to 126 shoots per m^2 (23 + 103) more on the grazed area. Differences of such magnitudes, based on the average weight per shoot in the exclosure, translate to −0.8 AUM/ha and 1.3 AUM/ha; they could influence grazing management. An AUM (animal unit month) is the amount of forage required by a mature cow with calf for one month (Range Term Glossary Committee 1974). We are also 95% confident that the maximum possible differences in spring were −4 shoots per m^2 to 134 shoots per m^2 more on the grazed area. A difference in the magnitude of the upper confidence limit could influence composition of the current forage crop. Confidence intervals for mature and juvenile shoots may be similarly interpreted.

RESIDUAL HERBAGE.—As expected, residual herbage of Nebraska sedge was greater (78 to 143 g/m^2) inside than outside the exclosure (Table 1). Residue outside in 1984 averaged 36% (24 to 56%) of that inside. Use of Nebraska sedge therefore averaged 64%. Leaving just 62 g/m^2 on the grazed area every year would not maintain site productivity.

The total amount of residual herbage should, however, be adequate to maintain productivity even with 64% use of Nebraska sedge each year. For the elevation of Tule Meadow, Ratliff et al. (1987) estimated that residual herbage should average 1,740 kg/ha for good condition wet meadows. Nebraska sedge is not the only species in the stand. Assuming equal use of all species and average production (474 g/m^2 in 1980–1981), we would expect residue outside the exclosure to total about 170 g/m^2 (1,700 kg/ha).

SHOOT HEIGHTS.—In spring, Nebraska sedge shoots within the exclosure were 41 to 67 mm taller in mean height than those outside (Table 1). Two explanations for this difference are offered. First, initiation of regrowth followed by cold weather may lower the carbohydrate reserves on the grazed area. This would lower the carbohydrate levels available for, and thereby slow, spring shoot growth. Second, grazing removes dead vegetation that insulates the soil surface and overwintering shoots. Insufficient insulation may keep temperatures below those needed for growth longer and thereby slow spring shoot growth.

By the time growth was completed in 1985, shoots looked equally high outside and inside the exclosure. If really the same, growth outside had to accelerate more than growth inside. Less shading of new growth outside by old leaf tissue could produce such an effect.

NUTRIENTS.—Concentrations of both nitrogen and potassium were greater in the residual herbage on the grazed area, but phosphorus concentrations were no different (Table 1).

Residual Nebraska sedge herbage on the grazed area still contained sufficient protein for cow maintenance. Herbage inside the exclosure was deficient in protein. Mean crude protein concentration (N% × 6.25) in residual herbage was between 0.3 and 1.3% more outside than inside the exclosure. Inside the exclosure the upper confidence limit for crude protein content was 5.8%. Outside the exclosure the lower confidence limit for crude protein content was 5.9%; the upper limit was 6.7%. Dry, pregnant, mature cows (the expected condition as the grazing season ends) require 5.9% protein in their diet (Church 1984).

Phosphorus concentrations were deficient for cow maintenance both inside and outside the exclosure. Diets of dry, pregnant, mature cows should contain at least 0.18% phosphorus (Church 1984).

Potassium requirements for cows are from 0.5 to 0.7% (Church 1984). Therefore, residual herbage inside and outside the exclosure has ample potassium for cow maintenance. Nevertheless, the difference in potassium between the exclosure and the grazed area is biologically significant. Potassium tends to concentrate in growing plant tissue (Black 1957, Church 1984). Higher potassium concentration in shoots from the grazed area suggests greater fall growth outside than inside the exclosure. Fall growth could negatively affect carbohydrate reserves needed for winter respiration and early spring growth.

CONCLUSIONS

By altering grazing patterns, weather at Tule Meadow appears to offset adverse effects of grazing on Nebraska sedge. Grazing in the 1984 dry season did not stimulate vegetative reproduction but did slow shoot growth the following spring. Shoot frequency and density were little affected, however, suggesting that occasional seasons of significant herbage removal have no lasting effects.

After grazing, less abundant, but more nutritious, forage is available for animals using the Nebraska sedge site in fall. Availability of nutritious fall forage may benefit wild herbivores, especially in dry years.

Grazing of Nebraska sedge should aim to remove excessive amounts of old leaf tissue and promote growth of new, photosynthetically efficient tissue. Management plans for grazing Nebraska sedge should, nevertheless, include end-of-season regrowth periods to assure ample carbohydrate reserves for winter respiration and initial spring growth.

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DIAMOND POND, HARNEY COUNTY, OREGON: VEGETATION HISTORY AND WATER TABLE IN THE EASTERN OREGON DESERT

Peter Ernest Wigand[1]

ABSTRACT.—Cores obtained in 1978 from Diamond Pond, Diamond Craters, Harney County, Oregon, as part of the Steens Mountain Prehistory Project, provide a record of vegetation change on the sagebrush/shadscale ecotone and of local and perhaps regional water tables. Pollen, macrofossils, sediments, and charcoal from these radiocarbon-dated cores were analyzed. Varying abundance of juniper, grass, sagebrush, and greasewood pollen, and of aquatic to littoral plant macrofossils reflects changing regional effective moisture and local water table since 6000 B.P.

Eleven dates spanning 5200 radiocarbon years and four regionally correlated volcanic ashes establish the dating of seven periods of different moisture regimes:

1. Greasewood and saltbush pollen dominance before 5400 B.P. indicates shadscale desert. Rapid accumulation of alternating silts and medium sands lacking aquatic plant macrofossils and pollen reflects periods of ephemeral ponds with water table 17 m below the present level and considerable erosion of maar slopes.
2. Increasing sagebrush pollen from 5400 to 4000 B.P. indicates sagebrush expansion into shadscale desert. *Scirpus*, *Rumex*, *Ceratophyllum*, and *Polygonum persicaria* macrofossils and finely laminated clayey silts evidence perennial pond.
3. From 4000 to 2000 B.P. abundant juniper and grass pollen reflects extensive juniper grasslands (juniper seeds from trees growing nearby fell into the pond during this period). Rising charcoal values indicate greater importance of fire. Deepest late-Holocene pond ca 3700 B.P. corresponds with postulated intensive human occupation of northern Great Basin marsh and lake locales.
4. Between 2000 and 1400 B.P. increased sagebrush pollen mirrors reduced effective moisture and reexpanding sagebrush steppe. More abundant *Scirpus* and *Rumex* macrofossils evidence shallow pond.
5. From 1400 to 900 B.P. more numerous grass pollen indicates returning greater effective moisture resulting in deeper water with abundant *Potamogeton*.
6. About 500 B.P. increased greasewood and saltbush pollen evidences drought. *Ruppia* seeds and pollen and the mollusk *Musculium* indicate shallow, brackish water.
7. Abundant juniper and grass pollen reflects moister conditions between 300 and 150 B.P. Numerous *Ceratophyllum* fruits indicate deeper, freshened water. Since the mid-1800s man and changing climate have encouraged sagebrush reexpansion. Increased *Scirpus* macrofossils indicate shallower water.

Although topographic diversity creates the variety of habitats found in the Great Basin, volcanic eruptions, tectonic activity, and sharp variations in climate, lasting 100 to 200 years, have affected the size and diversity of these habitats (Mehringer 1986, 1977). Climatic change in the Great Basin, especially in the north, is best reflected in its fluctuating lakes and marshes (Mehringer 1986).

Since early in 1826 when Antoine Sylvaille and five other trappers entered the Harney Basin of southern Oregon (Fig. 1) and reached the river later named for him—the Silvies River (Rich et al. 1950)—the volumes of Malheur and Harney lakes have varied considerably (Piper et al. 1939). Accounts from early trappers, descriptions by early settlers, and records maintained by local, state, and federal agencies reveal dramatic changes in the levels of Malheur and Harney lakes during the past 160 years.

Diamond Pond in the Diamond Craters area of the southern Harney Basin, Oregon, is an ideal location to watch changing vegetation patterns for three reasons. First, Diamond Pond lies adjacent to and at the same elevation as Diamond Swamp (Figs. 2, 3), and its water level is controlled by groundwater discharge. Second, varying abundance of aquatic and littoral plant macrofossils reflects the expansion and contraction of the fringe of littoral and emergent aquatic species that presently surround Diamond Pond (Fig. 3). Finally, changes in the shadscale, lower sagebrush, and juniper communities that adjoin on portions of Diamond Craters (Fig. 2) are reflected in the detailed microfossil record of vegetation change unparalleled in the northern

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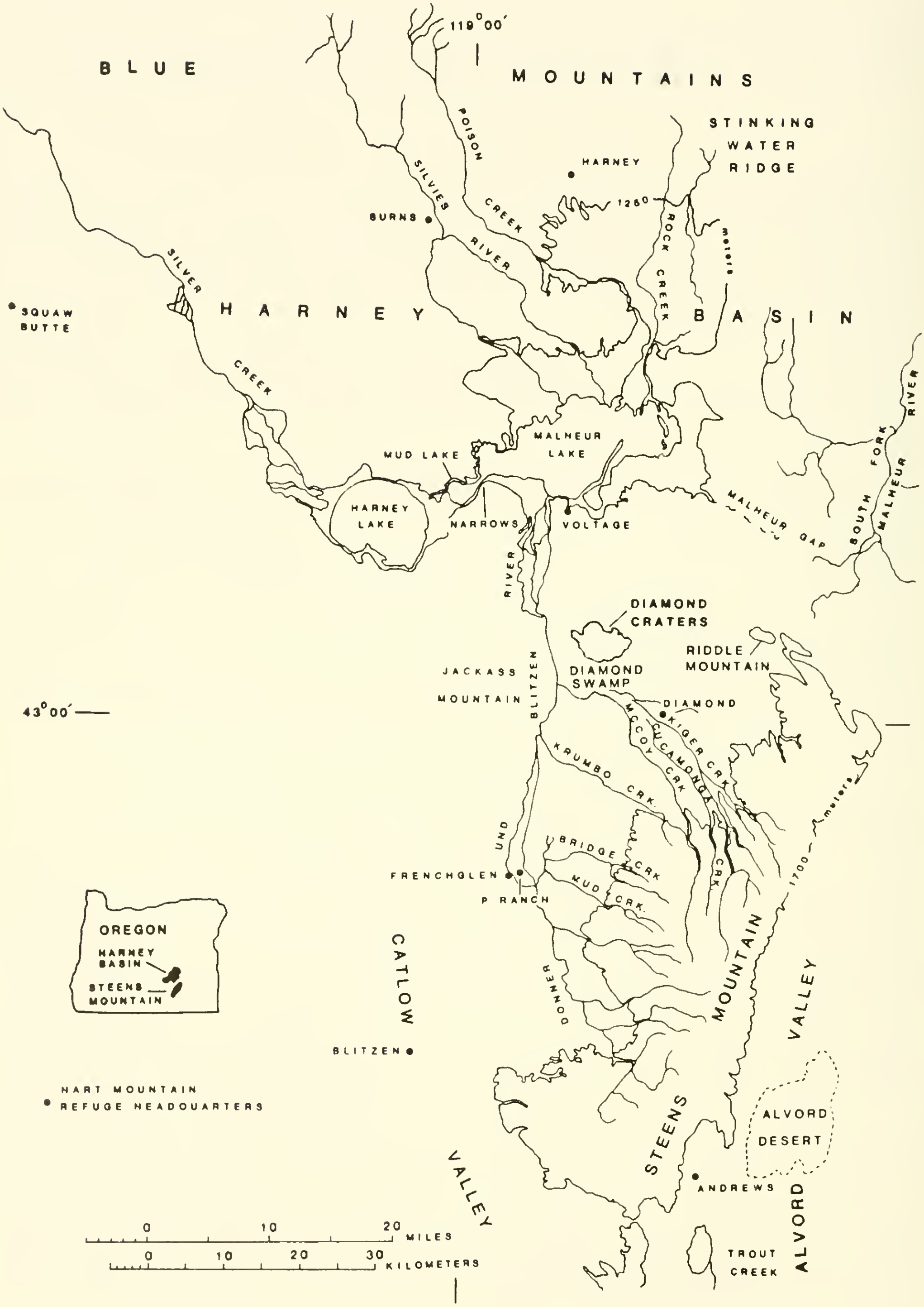
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BLUE MOUNTAINS
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SILVER CREEK
SQUAW BUTTE
HARNEY BASIN
MALHEUR LAKE
MUD LAKE
HARNEY LAKE
NARROWS
VOLTAGE
MALHEUR GAP
SOUTH FORK MALHEUR RIVER
RIVER
DIAMOND CRATERS
RIDDLE MOUNTAIN
JACKASS MOUNTAIN
BLITZEN
DIAMOND SWAMP
DIAMOND
43°00′
KIGER CRK
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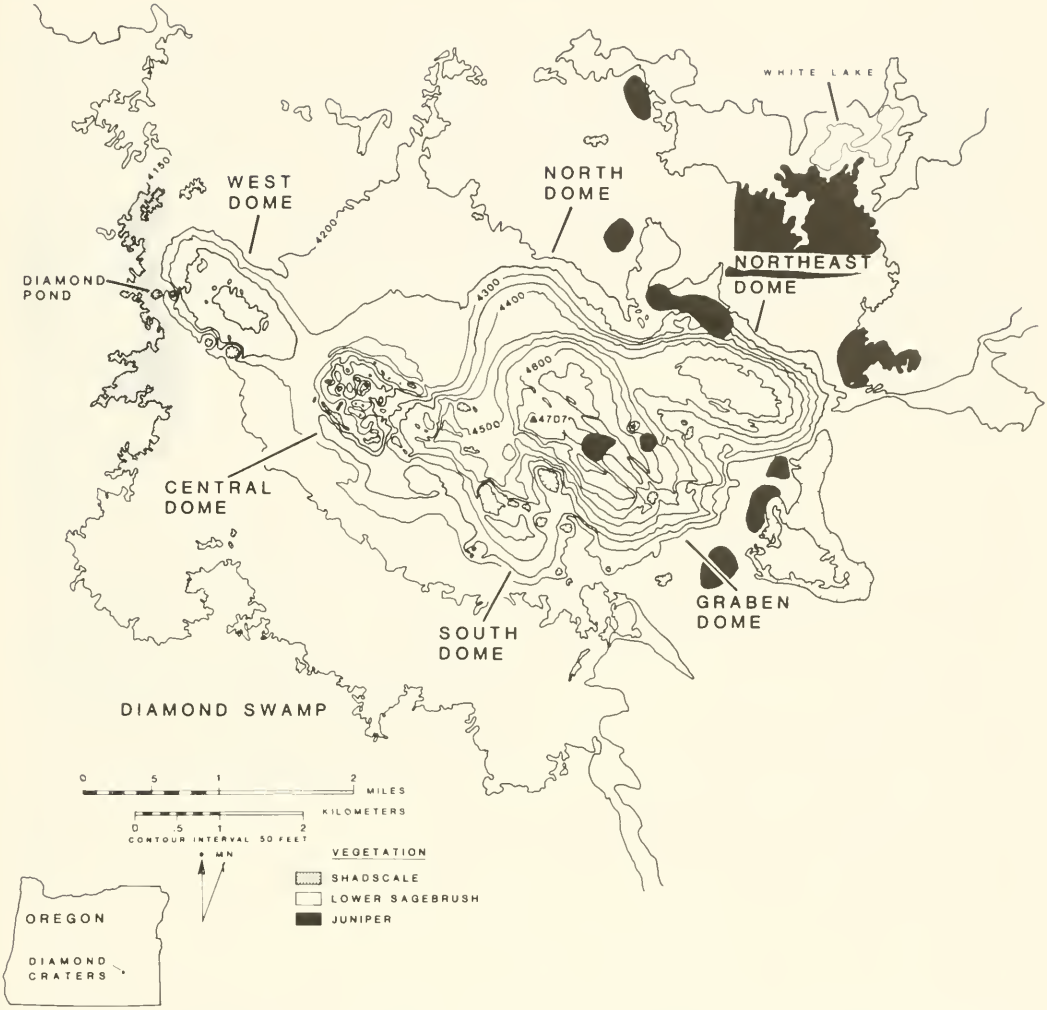
CUCAMONGA CRK
KRUMBO CRK
UND
BRIDGE CRK
FRENCHGLEN
P RANCH
MUD CRK
1700
meters
OREGON
HARNEY BASIN
STEENS MOUNTAIN
CATLOW
DONNER
MOUNTAIN
VALLEY
BLITZEN
HART MOUNTAIN REFUGE HEADQUARTERS
STEENS
ALVORD DESERT
ANDREWS
VALLEY
ALVORD
TROUT CREEK
0 10 20 MILES
0 10 20 30 KILOMETERS

Fig. 1. The Harney Basin of southeastern Oregon lies northwest of Steens Mountain. The 1,250-m (4,100-ft) contour is 1.2 m below the highest beach ridge of Pluvial Lake Malheur and 4.3 m below the drainage divide in Malheur Gap to the south fork of the Malheur River (Piper et al. 1939:18).


WHITE LAKE
WEST DOME
NORTH DOME
NORTHEAST DOME
DIAMOND POND
4150
4200
4300
4400
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4600
4707
CENTRAL DOME
SOUTH DOME
GRABEN DOME
DIAMOND SWAMP
0 .5 1 2 MILES
KILOMETERS
0 .5 1 2
CONTOUR INTERVAL 50 FEET
MN
VEGETATION
SHADSCALE
LOWER SAGEBRUSH
JUNIPER
OREGON
DIAMOND CRATERS

Fig. 2. Diamond Craters, Harney County, Oregon, with its major geological features and vegetation associations.

Great Basin. At Diamond Pond both pollen and macrofossils provide sensitive proxy data of climatic change in the Harney Basin.

HISTORICAL LAKE LEVELS

Early accounts of the sizes of Harney and Malheur lakes vary considerably, due in part to the time of year when the valley was visited. The Hudson's Bay Company trappers that explored and trapped the Snake River country usually passed through the Harney Basin either in early summer when seasonal runoff was greatest or in late fall when lake levels would be at their yearly low.

The lakes were first described on 31 October 1826, when Peter Skeene Ogden, chief trader of the Hudson's Bay Company, and 35 men descended the Silvies River and discovered two lakes separated by a "ridge of land about an acre in width." A freshwater lake (Lake Malheur) about 1 mi wide by 9 mi long lay east of a salty lake (Harney Lake) about 5 mi wide by 10 mi long (Davies et al. 1961:19–22). The "Sylivills River" (Silvies River) and two other small streams fed the freshwater lake, while another small river (Silver Creek) flowed into "Salt Lake."

On 7 June 1827 Ogden returned to the Harney Basin and found the lakes much higher than in the previous fall and had to detour northward to avoid the flooded basins

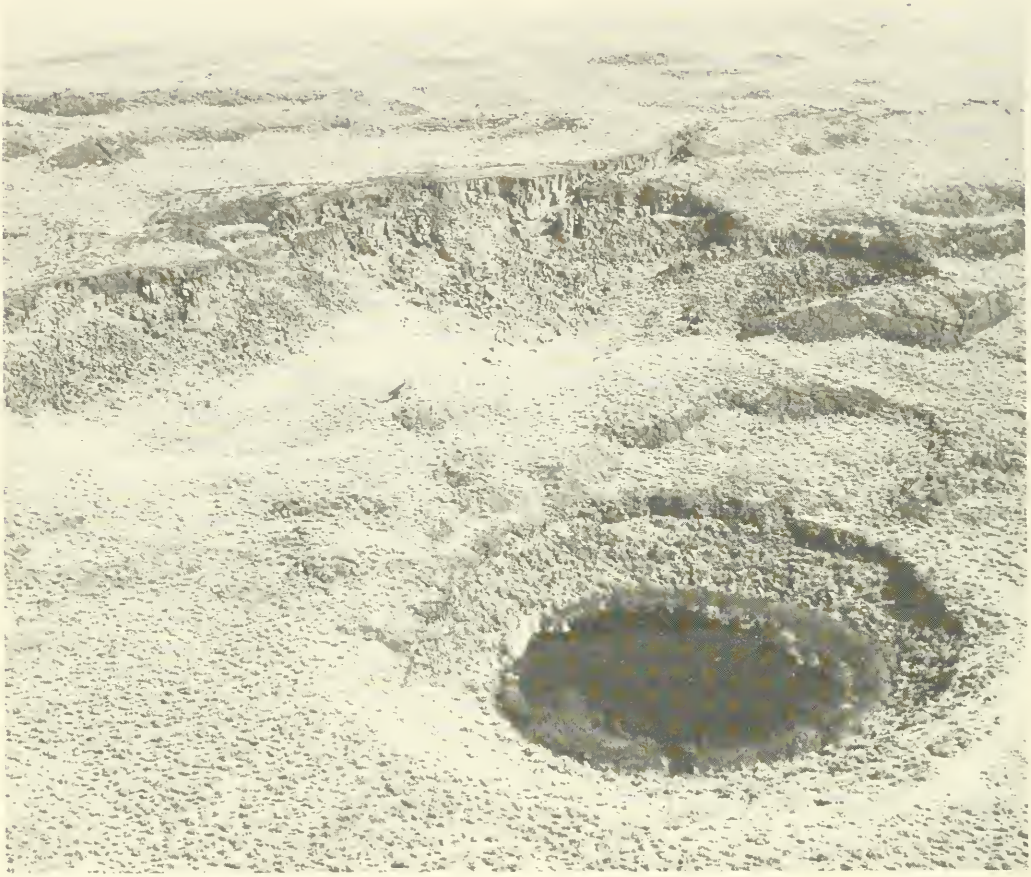

Fig. 3. Diamond Pond viewed from the northwest with the westernmost dome of Diamond Craters behind it (W. Bright photo, September 1978).

(Davies et al. 1961:125–127). On 18 and 19 June 1829 he ascribed a length of 20 mi (33 km) and a width of 15 mi (25 km) to "Sylvailles Lake" and a similar size to "Salt Lake" (Harney Lake) (Williams et al. 1971:160). A narrow ridge of land a few feet wide separated the lakes. These dimensions are larger than the basins that contain these lakes today.

Ogden's successor, John Work, camped next to "Sylvaille's Lake" (Malheur Lake) on 2 July 1831 and reported in his journal that the lake "was unusually high" and very brackish (Haines 1971:132). By 1833 maps of the area published by the London mapmaker, A. Arrowsmith, showed a chain of three lakes called the Youxpell Lakes (possibly Harney, Mud, and Malheur). Subsequently, the lake that was mistakenly thought to drain into the Malheur River was named Lake Malheur.

On 7 July 1859 Captain Henry D. Wallen reported "a large salt lake"—20 mi long by 9 mi wide. Wallen named it "Lake Harney" in honor of General Harney, who was commander of the military district of the Columbia (Clark 1932:111–112). Again these dimensions are much larger than the basin that contains Lake Harney. Despite the exaggerated accounts of Ogden and Wallen, Piper et al. (1939:22) suggest that prior to 1864 Malheur Lake may have been relatively small.

Since then Malheur Lake has nearly dried at least three times and has reached to or slightly beyond the meander lines of the official 1875 land surveys just as many times. According to various accounts, after three years of very low rainfall and runoff Lake Malheur was almost totally dry in 1889, and again in the fall of 1917 it was relatively small (Piper et al. 1939).

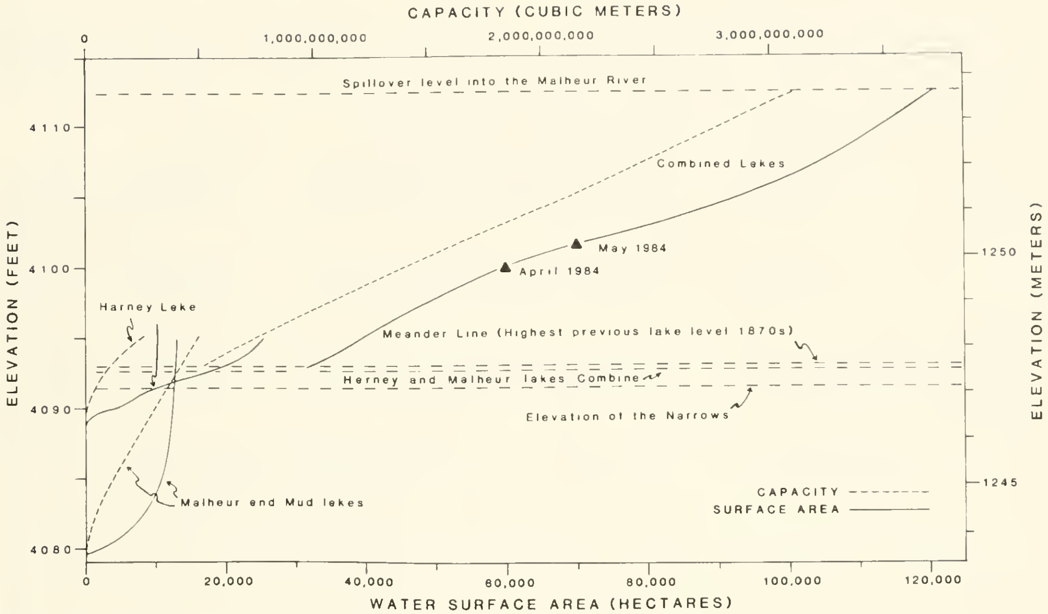

Fig. 4. Relationship of lake depth, surface area, and volume in the Harney Basin. At 1,254 m (4,114 ft) Malheur Lake would discharge into the south fork of Malheur River through Malheur Gap (Piper et al. 1939:18).

Desiccation beginning in 1921 culminated during the 1930s. In 1930 and 1931 no water ran into Malheur Lake from the Silvies River and very little from the Donner und Blitzen River. The lake began receding, and by September 1930 it covered only 810 ha (2,000 ac) (Fig. 4), and a year later only 203 ha (500 ac). In 1932 it still received no water from the Silvies River, but renewed flow from the Donner und Blitzen filled it to the 1,247-m (4,092-ft) level covering about 10,120 ha (25,000 ac). Excepting thermal springs on the lakebed, Harney Lake was dry during these three years. In 1934 both lakes were dry, and ranchers and farmers cut hay on the exposed bed of Malheur Lake (Ferguson and Ferguson 1978:17, 109). Again in 1966 through 1968 the lakes were almost dry (Walker and Swanson 1968:L13).

Large lakes characterized the late 1870s to early 1880s and recurred between 1895 and 1905 (Piper et al. 1939). In 1921 the lakes rose briefly before the extremely low levels of the 1920s and the total desiccation of the mid-1930s. After 1935 the lakes refilled and reached peak levels during the 1950s (Walker and Swanson 1968:L13). In early spring of 1984 the basins filled to form a lake some 60,700 ha (150,000 ac) in extent and, in places, over 10 m (30 ft) deep (Braymen 1984). At the 1984 rate of rise, with each meter increase in water depth covering an additional 11,290 ha (27,890 ac), the lake would have reached the 1,250-m (4,103-ft) level by June of 1985 and covered an area of about 81,000 ha (200,000 ac). However, drought conditions during the first half of 1985 and again during the first six months of 1986 and 1987 reversed this trend.

Fluctuating lake levels meant displacement and financial "boom or bust" for farmers and ranchers (Braymen 1984, Ferguson and Ferguson 1978:29–30, Crick 1983). Changing lake size and water chemistry dramatically affected both the extent of the marsh adjoining Malheur Lake and the flora and fauna within it (Piper et al. 1939:23).

STUDY AREA

The Landscape

Diamond Pond (SW1/4, Sec. 30, T28S, R32E, Diamond Swamp Quadrangle, Oregon) is a 2-m-deep, 46-m-wide perennial pond (Figs. 2, 3). It fills 92-m-wide Malheur Maar, an explosion crater, to within 9 m of the rim. The maar is located on the westernmost dome of the 67-km^2 Diamond Craters Volcanic Complex at 1,265-m elevation. To the southwest the confluence of Kiger, McCoy, and Swamp creeks and the Donner und Blitzen River form a broad, marshy floodplain, Diamond Swamp. The steep, east-facing side of fault-blocked Jackass Mountain lies to the west across the valley (Fig. 1). Northward stretches the Harney Basin with the broad expanses of the Malheur Marshes; beyond lie the rugged Strawberry Mountains. To the southeast is Steens Mountain (2,961 m) with its usually snow-covered crest 32–48 km from the craters.

Diamond Craters, first described by I. C. Russell (1903:54–57), is situated near the southern end of the Harney Basin, a 13,727-km^2 area of large-scale, post-Miocene subsidence into underlying magma chambers (Walker 1979:5–6). The craters consist of six major and one minor structural domes that range in height from 50 to 120 m and comprise an area over 9 km in diameter, which exhibits a variety of volcanic features (Peterson and Groh 1964, Brown 1980:12).

Surface drainage from the surrounding uplands collects in the north central part of the Harney Basin in two large, marsh-surrounded lakes periodically joined at the Narrows (Fig. 1). At its greatest extent in May and June, Malheur Lake typically extends 26–29 km eastward from the Narrows and is about 13 km across and up to 3 m deep (Waring 1909:11). When the water level in Malheur Lake exceeds 1,247.1 m (4,091.5 ft), it spills through the Narrows into Mud Lake. At 1,247.7 m (4,093.5 ft), Mud Lake overflows westward at Sand Gap into 11–13-km-wide Harney Lake (Piper et al. 1939:20–21). Although Harney Lake's depth may change up to a meter or more annually, its area is less variable because it lies in a steep-sided basin.

Silver Creek supplies Harney Lake from the northwest, whereas Malheur Lake receives runoff from the north through the Silvies River and Poison Creek (Piper et al. 1939; Hubbard 1975). To the south the Donner und Blitzen River and its tributaries originate on Steens Mountain where, during uplift and later Pleistocene glaciation, it eroded deep canyons in the gently dipping basalts (Russell 1903:17, 1905:84–85, Smith 1924, Fuller 1931:38, Hansen 1956:14, Bentley 1970:21, 67, 1974:213, 217, Mehringer 1985a:Fig. 12). Between Frenchglen and Diamond Craters the Donner und Blitzen River flows northward for 30 km through a verdant marshland from 0.5 to 5 km wide. North of Diamond Craters near Voltage it discharges into Lake Malheur (Fig. 1).

Climate

The topography of Harney Basin is the major factor influencing local climate. Elevation varies from 1,250 m on the valley floor to between 1,370 and 2,740 m in the surrounding uplands. The Harney Basin receives most of its precipitation from winter and spring storms derived from the marine air that flows into the Pacific Northwest (Fig. 5). Weather Bureau records collected since the late 1800s indicate that the Harney Basin as a whole is semiarid, but the Blue Mountains to the north and Steens Mountain to the south can receive up to three times the average regional precipitation. Snow, which accounts for about one-third of the annual precipitation, may fall on the valley floor between October and June and on the mountains in any month. The average annual total varies from 115 cm (45 in) at Burns to 64 cm (25 in) at the Harney Branch Experiment Station and 84 cm (33 in) at Diamond.

Daily and seasonal temperature range is wide, relative humidity is low, evaporation is great (about 4.8 times the annual rainfall; Piper et al. 1939), and the number of cloudless days per year averages about 120. The growing season varies from 80 days at the Harney Branch Experiment Station to 117 days at Burns. Although during the last 80 years annual mean temperature below 1,280 m (4,200 ft) in Harney Basin has averaged about 7.8 C (46 F), differences result from the peculiarities of local circulation. At Burns (1,267 m) over a 76-year period the mean January temperature was −3.8 C (25.1 F), and the mean July temperature was 19.8 C (67.6 F). The extremes ranged between −36 and 39 C (−32 and 103 F). Strong prevailing winds come from the southwest throughout the year, but especially during March through June (Martin and Corbin 1931, Sternes 1960, U.S. Department of Commerce, Weather Bureau 1954–1984).

Lake levels in the Harney Basin depend primarily upon the discharge of its four major streams (Fig. 6) and groundwater recharge (Russell 1903:29); however, they also mirror total precipitation. Precipitation amounts in

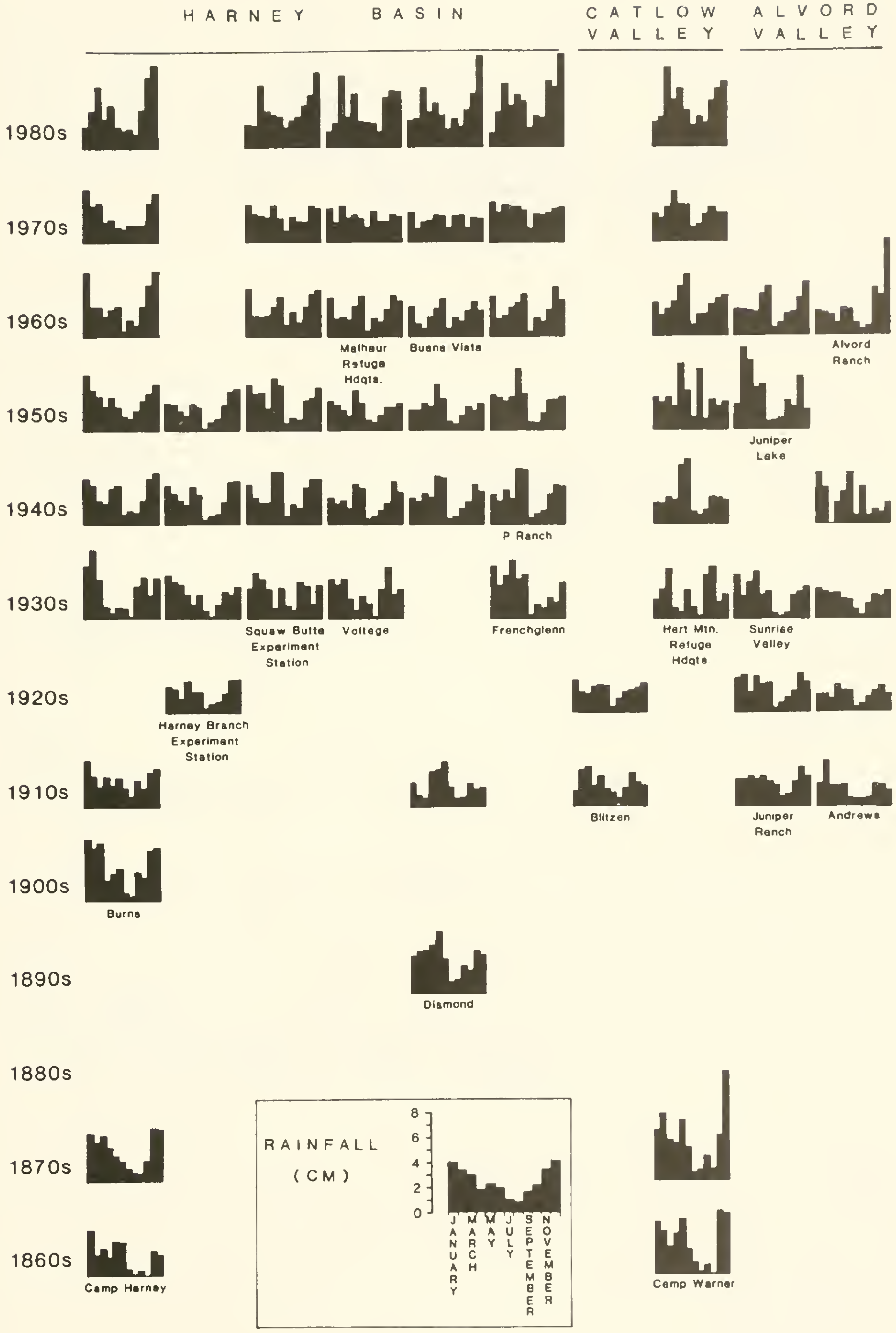

Fig. 5. Decadal means (e.g., 1971–1980) for monthly rainfall in the Harney Basin since the 1860s. Monthly averages for the 76-year Burns, Oregon, rainfall record are illustrated in the figure key (bottom center).

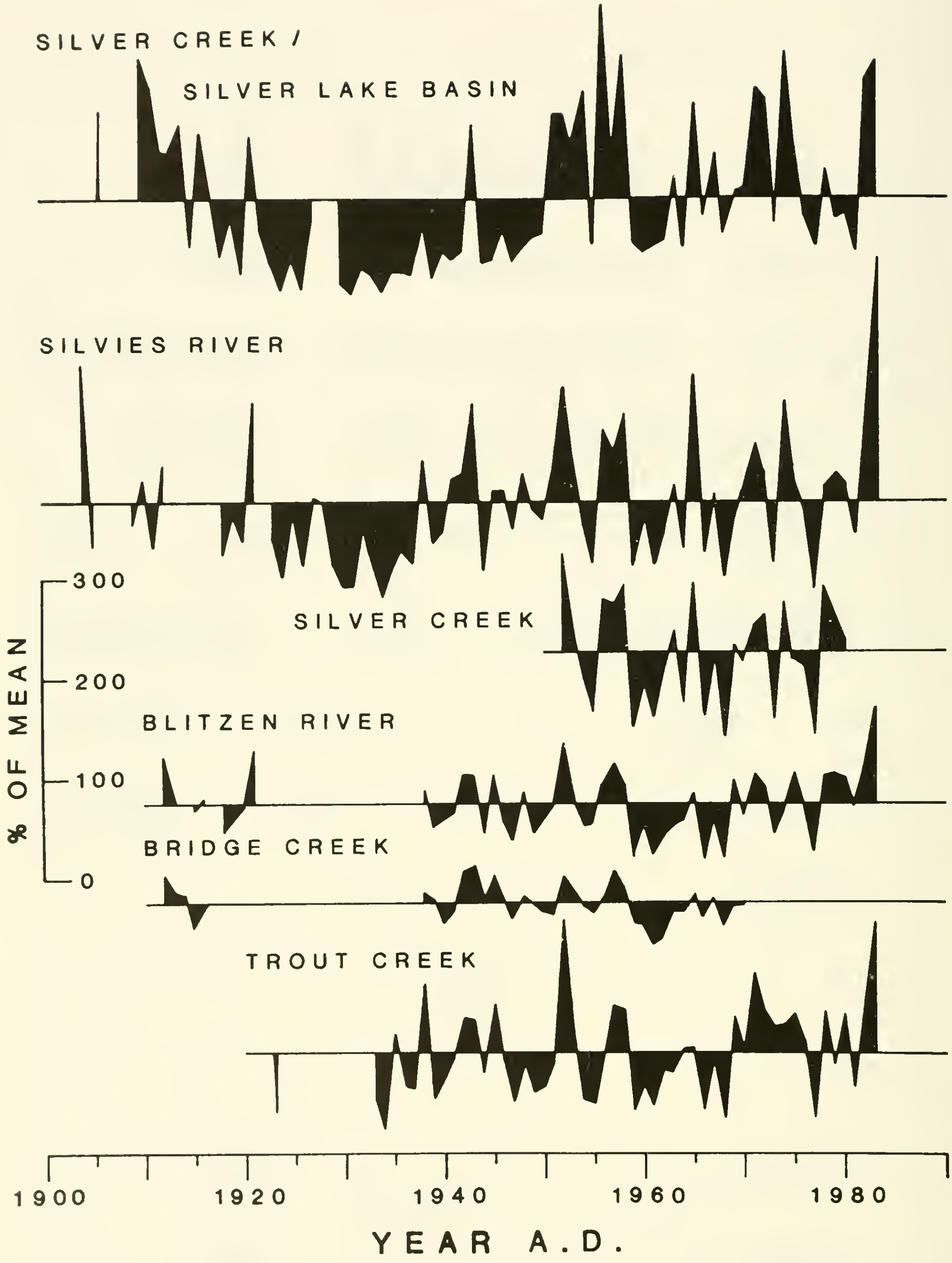

Fig. 6. Stream discharge records, expressed as percent of the mean for all years of record for major streams of the Harney Basin.

the Harney Basin and the Catlow Valley to the south show similar trends during the last 80 years (Fig. 7). Annual rainfall averages between 20 and 30 cm (8 and 12 in) a year in the Harney Basin. Recording stations along the western edge of the basin average about 30 cm

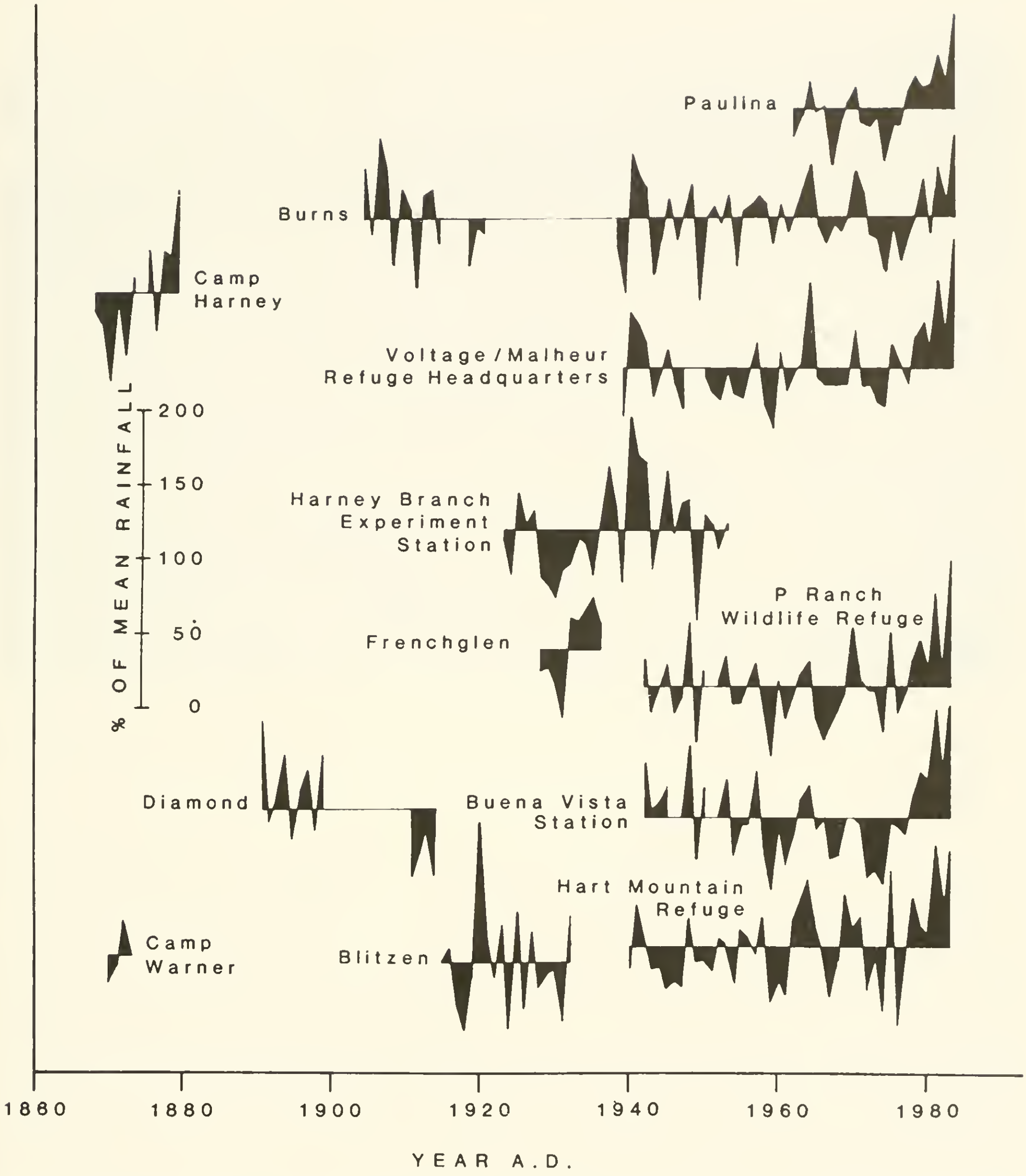

Fig. 7. Rainfall in the Harney Basin and the Catlow Valley expressed as a percentage of long-term means. The northernmost stations are at the top.

(12 in) annually, whereas stations located in the north central part of the basin average closer to 20 cm (8 in) annually.

Vegetation

The terrestrial flora of the Harney Basin reflects the environmental restrictions of a dry climate and thin, volcanic, often saline soils. Distribution of local plant communities varies according to characteristics of soil (depth, pH, and moisture), site (slope, aspect, and elevation), and temperature. On the surrounding mountains plant species from the Rocky Mountains, the Cascades, the Sierras, and the mountain ranges of the Great Basin combine with endemic species to form characteristic plant communities (Price 1978).

A transect between Diamond Craters and the top of Steens Mountain cuts across at least six distinct vegetation zones that have been

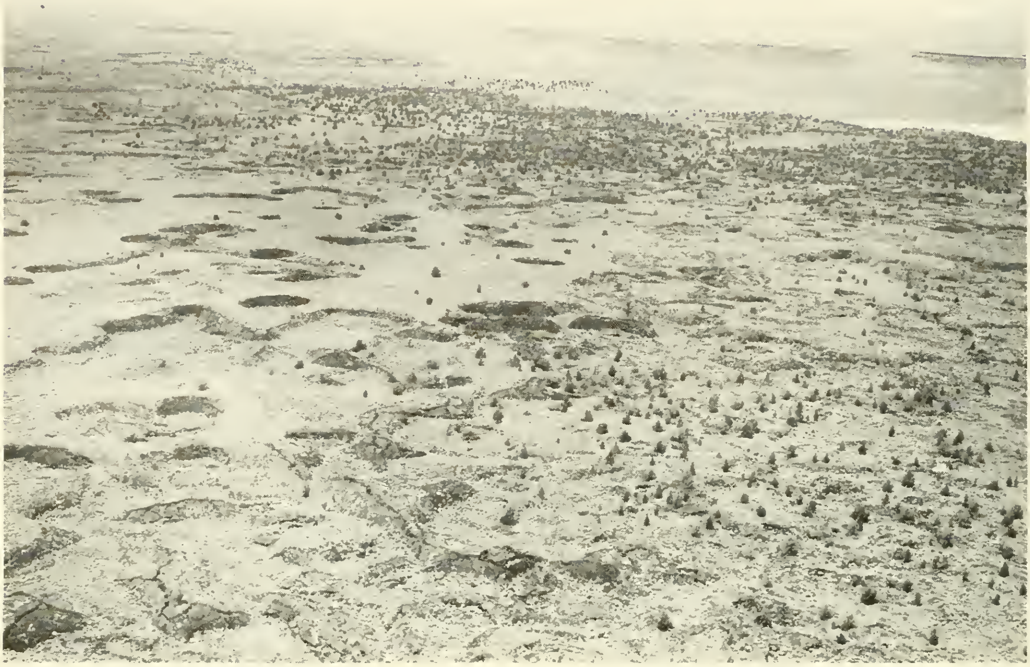

Fig. 8. View northward toward the lava flows northeast of Diamond Craters. The area between Northeast Dome and White Lake (upper right) has the densest stands of juniper on Diamond Craters (P. Wigand photo, June 1980).

studied and variously named during the past 30 years (Hansen 1956, Faegri 1966, Urban 1973, Mairs 1977). Generally, these zones from lowest to highest are: (1) the Shadscale Zone dominated by *Sarcobatus vermiculatus* (black greasewood), *Atriplex spinosa* (spiny hopsage), and *Atriplex confertifolia* (spiny saltbush); (2) the Lower Sagebrush Zone dominated by *Artemisia tridentata* var. *tridentata* (big sagebrush) but with abundant *Chrysothamnus nauseosus* (gray rabbitbrush), *C. viscidiflorus* (green rabbitbrush), *Tetradymia glabrata* (littleleaf horsebrush), and *T. canescens* (gray horsebrush); (3) the Juniper Zone characterized by *Juniperus occidentalis;* (4) the Aspen Zone with both *Populus tremuloides* (quaking aspen) and *Cercocarpus ledifolius* (mountain mahogany); (5) the Upper Sagebrush Zone dominated by *Artemisia tridentata* var. *vaseyana;* and (6) the Subalpine Grassland (Mehringer and Wigand 1987:Fig. 4). Of these, the Shadscale, Lower Sagebrush, and Juniper zones occur at Diamond Craters.

The Shadscale Zone occupies thin, stony soils on the south and west sides of West Dome (Figs. 2, 3). The Lower Sagebrush Zone covers most of Diamond Craters and supports, in addition to the dominant shrubs, a variety of grasses, including *Stipa comata* (needle-and-thread grass), *Stipa thurberiana* (Thurber's needle-and-thread grass), and *Bromus tectorum* (cheatgrass). The Juniper Zone covers the low-lying lava flows north of North Dome (Figs. 2, 8). Big sagebrush, *Holodiscus dumosus* var. *glabrescens* (gland ocean-spray), *Ribes cereum* (squaw currant), *Ribes aureum* (golden currant), rabbitbrush, ferns (in moist crevices in the lava flows), and native bunchgrasses, primarily *Agropyron spicatum* (bluebunch wheatgrass), grow among junipers that, according to counts of tree rings collected by personnel of the Bureau of Land Management (BLM), are up to 200 years old.

Diamond Pond lies within the ecotone between shadscale and lower sagebrush communities on Diamond Craters. The terrain east and south of Malheur Maar is dominated by big sagebrush and its associates. North and west of the maar black greasewood and spiny hopsage intermingle with big sagebrush, littleleaf horsebrush, *Tetradymia spinosa* (spiny horsebrush), and some *Artemisia spinescens* (bud sage). Growing among the shrubs are *Leptodactylon pungens* (prickly phlox), *Chaenactis douglasii* var. *achilleaefolia* (dusty maiden), and tidytips (*Layia glandulosa*).

Within Malheur Maar aspect determines whether shadscale or big sagebrush communities predominate. Whereas the south-facing slope supports spiny saltbush, some spiny hopsage, and an occasional big sagebrush or green rabbitbrush, the east- and north-facing slopes are covered by green rabbitbrush and big sagebrush interspersed with hopsage and occasional spiny saltbush. The west-facing slope consists of a talus with a few big sagebrush and bunches of giant wildrye (*Elymus cinereus*). A single golden currant survives in the shade offered by the cliff on the north-facing slope of the maar.

Between the shrubs of the south-facing slope are *Amsinckia tessellata* (tessellate fiddleneck), *Cryptantha circumscissa* (matted cryptantha), *Cryptantha torreyana* (Torrey's cryptantha), and *Astragalus lentiginosus* (freckled milkvetch). A dense blanket of *Distichlis stricta* (alkali saltgrass) and bunches of borax weed (*Nitrophila occidentalis*), saltwort (*Glaux maritima*), and poverty weed (*Iva axillaris*) thrive on the lower slope close to the water's edge.

Bromus tectorum (cheatgrass) occurs throughout the maar. *Oryzopsis hymenoides* (Indian ricegrass) and *Sitanion hystrix* (bottlebrush squirreltail grass) are locally abundant along the northwest rim of the maar, and tufts of *Muhlenbergia asperifolia* (alkali muhlenbergia) and pockets of the exotic grasses, *Bromus japonicus* (Japanese bromus) and *Agropyron cristatum* (crested wheatgrass), occur sporadically on the slopes of the maar.

Growing close to the western and northwestern margins of the pond are stands of European and native weeds. *Urtica dioica* ssp. *gracilis* var. *angustifolia* (stinging nettle) and *Lepidium latifolium* (pepperwort) predominate, with some *Cirsium arvense* (Canadian thistle), *Epilobium minutum* (willowherb), *Aster frondosus* (short-rayed aster), *Solidago occidentalis* (western goldenrod), and in open, sunny areas *Potentilla anserina* (common silverweed) and *Chenopodium album* (pigweed).

In the moist ground at the water's edge and in the shallow water of the pond's margins grow *Rumex maritimus* (golden dock), Ranunculus cymbalaria (*shore buttercup*), *Veronica anagallis-aquatica* (water speedwell), and *Juncus balticus* (Baltic rush). *Typha latifolia* (common cattail) lining the northern and western margin of the pond is broken by a stand of *Phragmites communis* (common reed) on the northeast shore. Along the north shore the cattails are enclosed by a stand of *Scirpus acutus* (hardstem bulrush) that dominates the southern, western, and northern shores of Diamond Pond. Thick growths of *Ceratophyllum demersum* (hornwort) and *Potamogeton pectinatus* (sego pondweed) clog the pond.

Methods

In June 1978 a crew that included Dr. P. J. Mehringer, Jr., K. L. Petersen, myself, and members of the Steens Mountain Prehistory Project summer field school began coring near the center of Diamond Pond. Dr. Mehringer and students from the Department of Anthropology's fall 1978 palynology class completed coring in late October of the same year (Fig. 9). We obtained 14.97 m of core with a modified Livingston piston corer (Cushing and Wright 1965) that was operated from a drive tower anchored to a wood and styrofoam raft. Overlapping cores were collected for the top 5.45 m. After collecting each core in 3-m-long, 10-cm-diameter barrels, we cut them to the actual length of sediment recovered, capped them, and returned them to cold storage at Washington State University.

Prior to description and sampling, we exposed the sediments by cutting the barrels lengthwise with a rotary saw, thereby avoiding distortion of sediments by extrusion. Cores were correlated by distinctive stratigraphic markers, especially volcanic ashes, and by depth. Generally, our sediment description adhered to Soil Survey Manual (Soil Survey Staff 1951) except that boundary distinctness followed Mehringer and Sheppard (1978). We determined color (moist and dry) with the Munsell Soil Color Chart (1975). Sediments with recurrent series of texture differences are denoted as laminae, whereas sequences of similar texture but different color are denoted as bands.

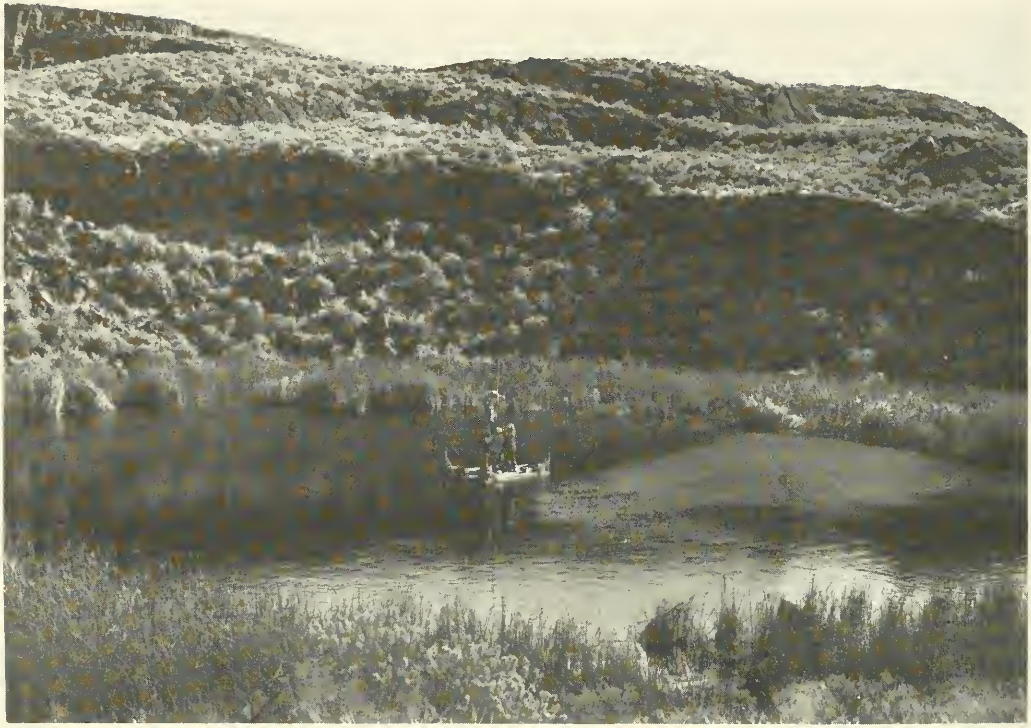

Fig. 9. WSU Department of Anthropology palynology class coring Diamond Pond (October 1978). View is to the southeast. Far slopes are dominated by sagebrush. Hardstem bulrush (*Scirpus acutus*) and cattail (*Typha latifolia*) are visible in the foreground.

Before sampling the cores for micro- and macrofossils, we removed 11 radiocarbon and 4 tephra samples to establish a regional sequence of dated volcanic ashes (Mehringer et al., in preparation). Microfossil sampling interval was determined by depth, sediment type, boundary location, and apparent age. Several replicate samples were collected from each of 312 levels by removing a 1 × 1 × 2-cm block (2 cm^3) with a wire frame cutting device (Kolva 1975:Fig. 6), or, in a few cases where this was not possible, sediments were packed into a round-bottomed scoop with a volume of 2.3 cm^3 (Fletcher and Clapham 1974, Bartholomew 1982:15). We used one replicate sample from each level for microfossil analysis and another to determine dry weight and organic and carbonate carbon percentages by weight loss on ignition at 600 and 950 C (Dean 1974).

Pollen extraction generally followed Mehringer (1967:137); after acetolysis the samples were mounted in silicone oil (2000cs). To estimate the number of microfossils per volume of sediment, we added 10 commercially prepared tablets, each containing 10,850 ± 200 *Lycopodium* spores (batch no. 006720) (Stockmarr 1971, 1973), and weak HCl to all but 24 samples as the first extraction procedure. The 24 samples, from near the top of the sequence, were extracted as part of a pollen class project in fall of 1978. Ten tablets, each containing 12,500 ± 500 *Lycopodium* spores (batch no. 212761), were added to each of these samples.

Using 400X magnification, I counted 96 samples from Diamond Pond with a range of 406–2,937 terrestrial pollen (mean 949 ± 543) and 104–3,281 *Lycopodium* tracers (mean 612 ± 456) (Fig. 10). With the addition of aquatic pollen types and spores, counts range from 436 to 3,359 (mean 1,135 ± 577). When the algae are added, the number of microfossils per sample ranges from 471 to 4,400 (mean ca 2,000). In a few cases the algae were so abundant that their numbers had to be approximated from the number of algae observed while counting at least 200 *Lycopodium* tracers. In addition, two sizes of charcoal, Charcoal A (25–50 microns) and Charcoal B (> 50 microns), were counted.

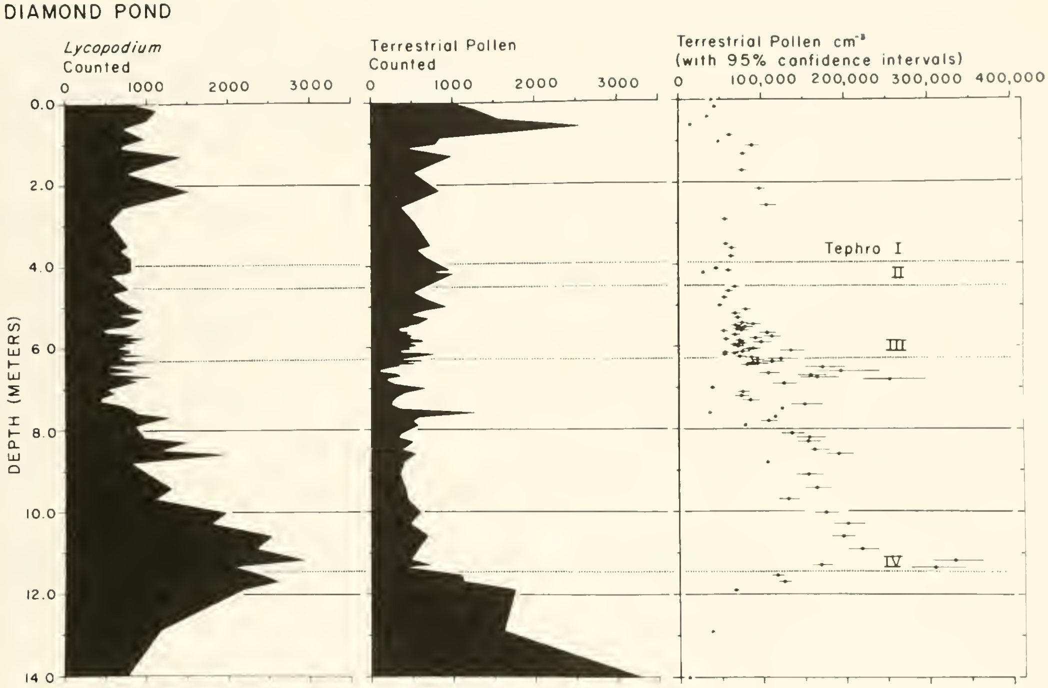

Fig. 10. Number of *Lycopodium* tracers and terrestrial pollen counted per sample and the population estimates of terrestrial pollen (pollen sum) per cubic centimeter of sediment.

As a standard procedure during analysis of the Steens Mountain lakes, at least 50 grains each of grass, sagebrush, saltbush, greasewood, and pine pollen were counted because they were to be used in ratios providing important clues to the history of steppe vegetation. Often the number of pollen grains counted was determined by attaining at least 50 grass pollen.

After sampling for microfossils, we cut one complete sequence of cores into sections corresponding to stratigraphic units or, when stratigraphic units exceeded 15 cm, into equal subdivisions of the unit not longer than 15 cm. We used two-thirds of each of these samples for macrofossil analysis and the other one-third for sediment analysis.

One hundred and thirty-five macrofossil samples of known volume (determined by displacement of water) were washed through four nested, stainless steel screens (8, 10, 28, and 42 meshes per inch). Initially, I separated the residue by size and removed the most obvious seeds and shells. Later, using a dissecting microscope, I sorted the still-moist fractions and identified macrofossils by comparing them with the seed and plant collections of the Laboratory of Anthropology and the Marion Ownbey Herbarium, Washington State University, and standard texts (Martin and Barkley 1961, Berggren 1969, Montgomery 1977, Katz et al. 1965, Musil 1978). After identifying the macrofossils, I dried them for storage and future radiocarbon dating. Shells of the mollusks *Lymnaea palustris*, *Planorbella subcrenata*, *Gyraulus parvus*, *Gyraulus crista*, and *Musculium securis* were identified by Dr. Dwight W. Taylor.

Following routine pretreatment to remove carbonates (hydrochloric acid) and organic matter (hydrogen peroxide) (Black 1965:559, 562), I employed wet screening and hydrometer methods to divide 33 sediment samples at 0.5-phi intervals into 26 size classes ranging from −2.0 to 11.0 phi (Krumbein 1934). The resulting cumulative weight percentage curve was used to determine mean, median, sorting, skewness, and kurtosis (Folk and Ward 1957).

I entered all data on computer files for statistical analyses and computer plotting. To facilitate presentation and discussion of the

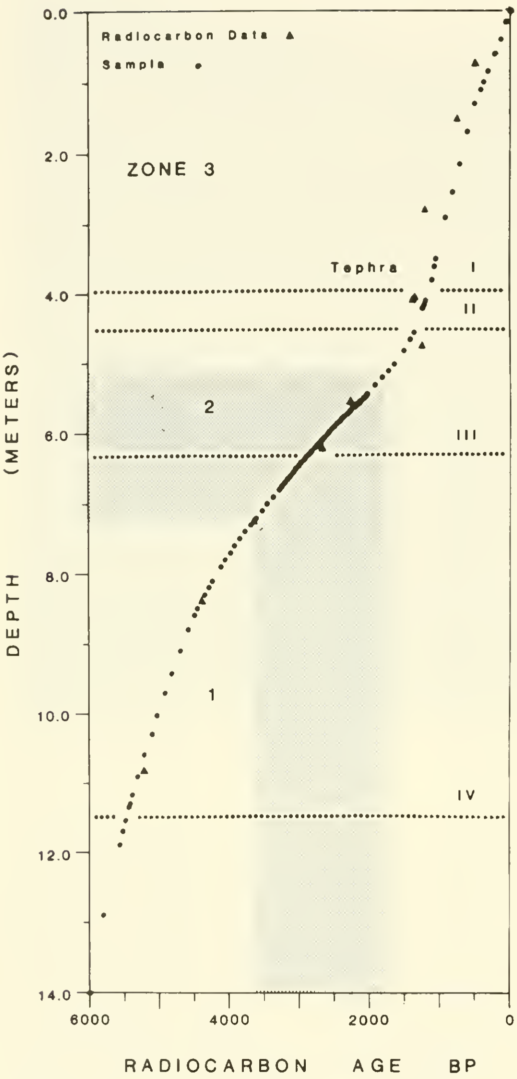

Fig. 11. Pollen samples with respect to depth, radiocarbon age B.P., and pollen zones.

micro- and macrofossils, I subdivided the diagrams into zones by using a cluster analysis program that joined only neighboring samples or adjacent groups into a dendrograph (Orloci 1967, Petersen 1981:45–46).

Both to summarize and illustrate major changes in the micro- and macrofossil records, I plotted ratios of specific plant species by radiocarbon age. Ratios selected for Diamond Pond and other Steens Mountain lakes use the most abundant pollen types, usually from plants that characterize the vegetation zones of the Harney Basin and Steens Mountain. These ratios were calculated as a standard procedure for comparison of the microfossil data for all Steens Mountain Project pollen counts. All pollen and charcoal ratios presented were smoothed using a three-level weighted average, (a+2b+c)/4 (Holloway 1958).

Results

Dating and Deposition Rate

Eleven radiocarbon determinations and four regionally correlated tephras from Diamond Pond cores establish a chronology spanning the last 5500 years B.P. and provide a basis for the deposition rate curve (Fig. 11). Except between ca 4500 and 1500 B.P. when deposition slowed, sediment has accumulated rapidly since 6200 B.P.

Modern *Ceratophyllum demersum* from Diamond Pond dating 126 ± 1.6% modern (WSU-2529) agrees with postbomb modern samples of the last six years or so (Baker et al. 1985). This indicates that groundwater supplying Diamond Pond today does not contain old carbonates that might result in erroneous radiocarbon dates.

Sediments

Diamond Pond deposits above 11.4 m (ca 5450 B.P.) primarily consist of dark, laminated, fine silty clay rich in organic detritus and well-preserved macrofossils (primarily seeds and snail shells). Laminated inorganic clays, silts, and sands with occasional lenses of sandy fine gravel containing angular and spherical clay clasts characterize sediments below 11.4 m.

Grain size analyses of 33 sediment samples from Diamond Pond indicate occasional increases in sand content resulting in a much coarser median and mean grain size, poorer sorting, and more positive skewness (Fig. 12). Above 11.4 m sediments with finer mean and median grain size reflecting increased silt and clay content are typical. Characteristically, these sediments are less positively skewed, better sorted, and more leptokurtic than those below 11.4 m. However, at least three units of coarser sediment interrupt these finer deposits.

Organic and Carbonate Content

Plots of weight loss on ignition of 312 samples (Fig. 13) show a gradual increase in or-

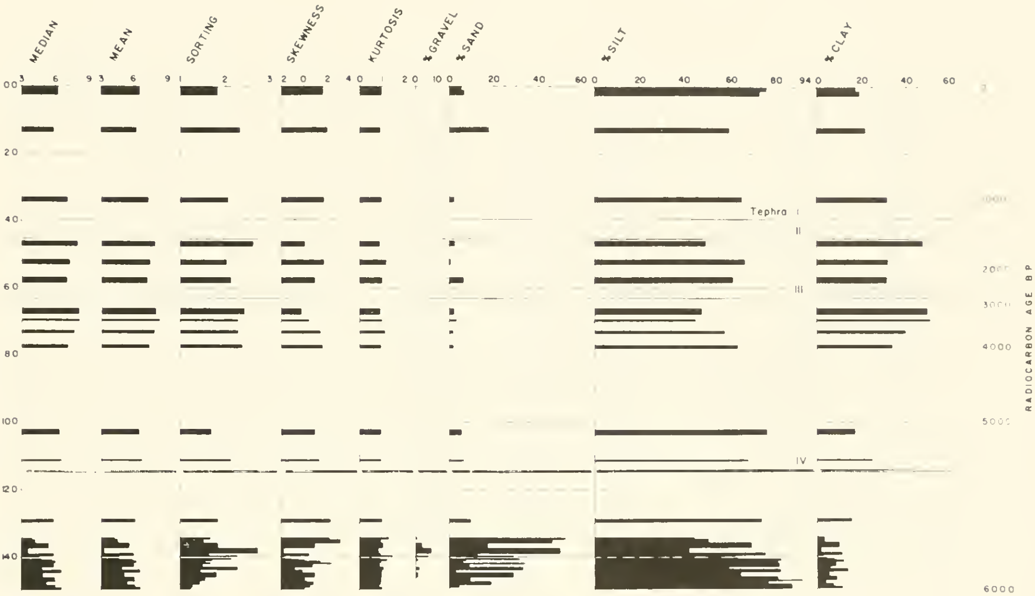

Fig. 12. Sediment parameters and proportions of gravel, sand, silt, and clay.

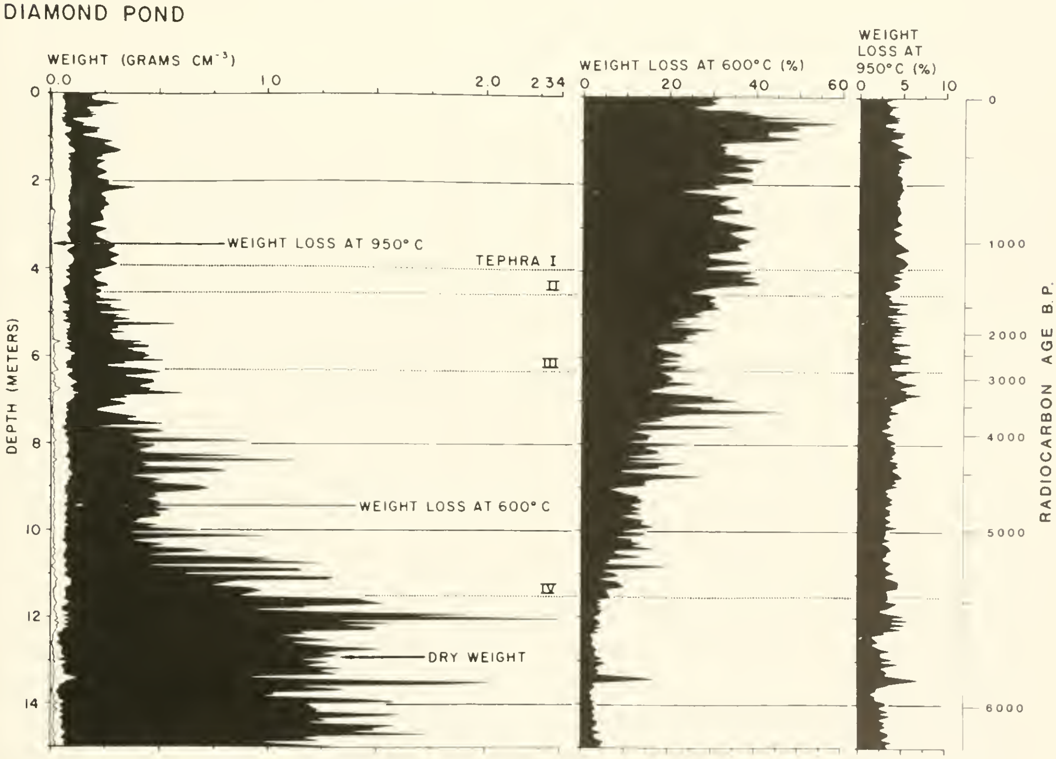

Fig. 13. Weight loss on ignition (first axis), and organic carbon (second axis) and carbonate (third axis) percentages from 312 samples from Diamond Pond. Note that organic carbon weight on the first axis is the difference between weight loss at 950 C and weight loss at 600 C.

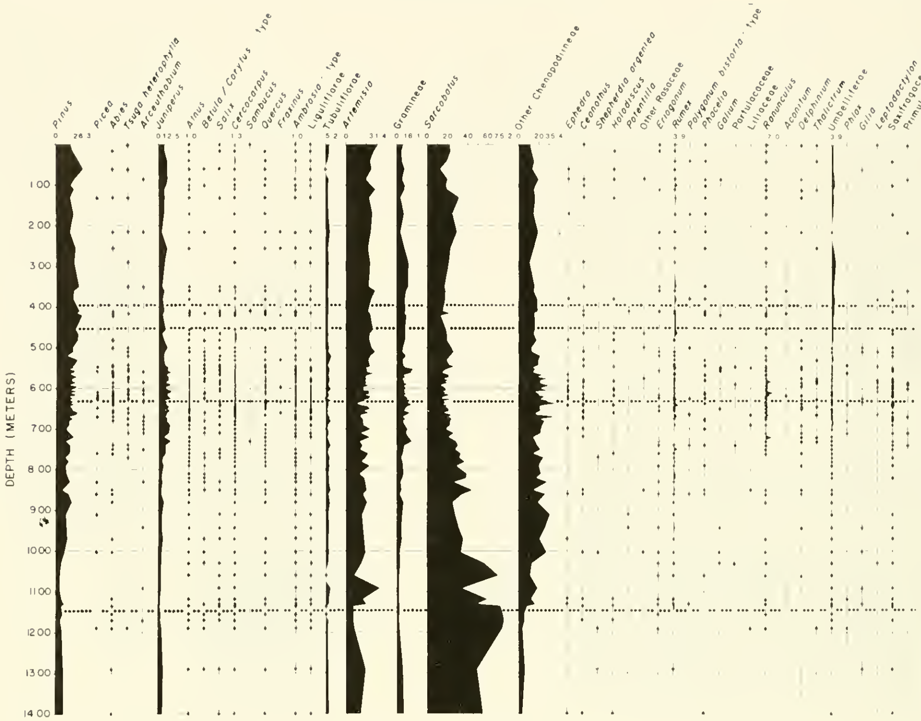

Fig. 14. Relative percentage diagram of all microfossils plotted by depth.

ganic matter from about 6200 B.P. to the present. Organic carbon percent remains low below 11.4 m (ca 5450 B.P.) when the first significant increase occurs. Organic carbon percent reached its maximum within the past 300 years.

Carbonate percentages are less than 2% below 11.4 m. Above 11.4 m they generally vary between 1 and 6%. Increases in carbonate content may reflect major variations in water table or water chemistry that reflect significant climatic change.

Microfossils

Sixty-six pollen types, of which 11 were from aquatic or emergent aquatic plants, were identified (Fig. 14). Although included in the terrestrial pollen sum, 3 other pollen types, *Rumex*, *Ranunculus*, and Umbelliferae, belong to genera with species that grow in water or poorly drained habitats. All terrestrial pollen types appear as a percent of total terrestrial pollen (pollen sum), whereas aquatic pollen types are expressed as a percent of the total of both terrestrial and aquatic pollen (total pollen).

All spores (except *Equisetum* and *Isoetes*, which are abundant and classed separately) are assigned to either monolete or trilete spore categories as a percent of total pollen. A large number of monolete spores compare favorably with *Cystopteris fragilis* (bladderfern). Most trilete spores were *Pteridium aquilinum*–type (bracken fern), although a few *Pilularia americana* (pillwort) spores were identified.

Algae, including *Botryococcus*, *Tetraedron*, five species of *Pediastrum*, and two unknown types of algae are plotted in the main diagram as percent of total pollen. Following the procedure adopted for the Steens Mountain Project, I divided charcoal into two categories, one of 25–50 microns and another of > 50 microns and plotted it as a percent of total pollen.

Pollen zones.—Three pollen zones, based upon the eight most common terrestrial plant pollen types (*Pinus*, *Juniperus*, *Artemisia*, Gramineae, *Sarcobatus*, other Chenopodiineae, Tubuliflorae, and Umbelliferae), are apparent in the dendrograph (Fig. 15). To eliminate the influence of aquatic and littoral plants on formation of the zones, they are excluded. In addition, the two lowest pollen

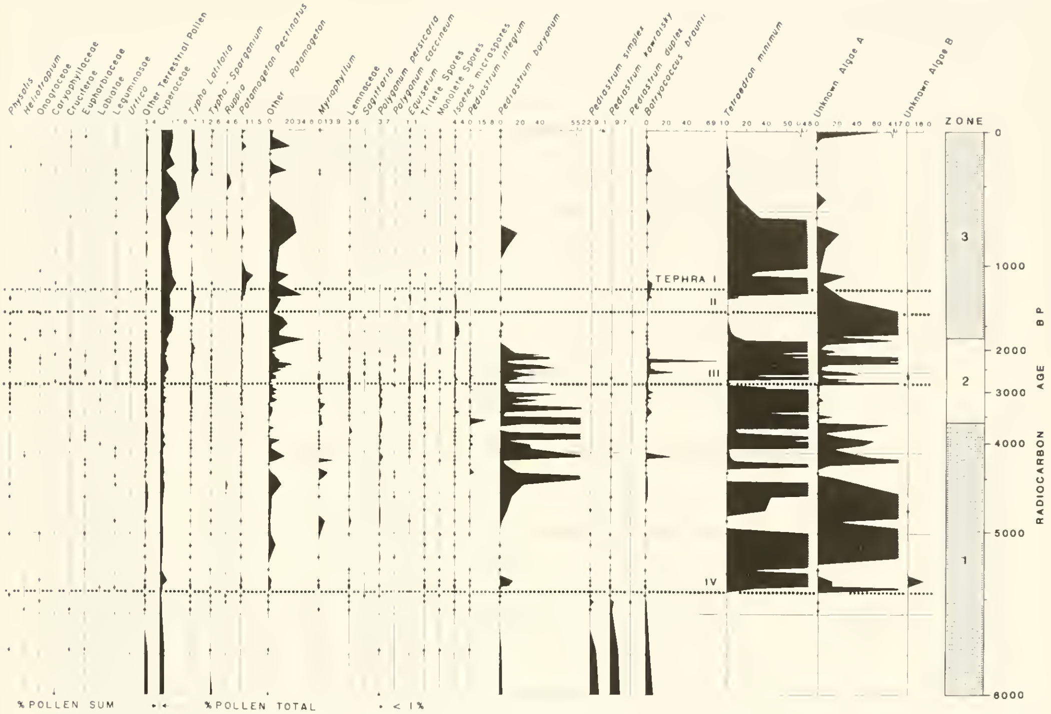

Fig. 14 continued.

samples, 12.9 m (ca 5800 B.P.) and 14.0 m (ca 6000 B.P.), were omitted from the sample set used for zoning because they contained pollen grains probably derived from Pliocene and Miocene deposits. Although other zone divisions are possible, the breaks at 7.25 and 5.15 m (ca 3630 and 1750 B.P.) are the most obvious and useful (Figs. 15, 11).

POLLEN ACCUMULATION RATES.—From the average years per centimeter for each zone and estimates of the total microfossils per sample, I calculated the number of microfossils deposited per square centimeter per year for each sample. Pollen accumulation rates for Zone 1 between 11.9 and 8.1 m and in Zone 3 between 3.8 and 0.85 m are from 3 to 10 times larger than the average for Zone 2 (Fig. 16). More pollen is accumulating in the sediment than can be accounted for given the time represented in Zones 1 and 3. Pollen accumulation rates for Zone 2 average about 10,000 pollen grains per cm^3 per year, rather than the 33,140 pollen grains per cm^3 per year estimated for Zones 1 and 3. Rapid pollen accumulation in Zones 1 and 3 corresponds with major increases in *Sarcobatus* pollen percentages and of sand in the sediments of Diamond Pond.

Macrofossils

I recovered macrofossils of 16 plant genera, along with five species of mollusks and two species of ostracods, from Diamond Pond (Fig. 17). Plant macrofossils include the well-preserved seeds and occasional fruits of terrestrial, aquatic, and littoral species.

Shells of the mollusks *Lymnaea palustris*, *Planorbella subcrenata*, *Gyraulus parvus*, *Gyraulus crista*, and *Musculium securis* occur primarily in Zones 1 and 3 but were not found in the present aquatic vegetation (Fig. 17). Living *Lymnaea palustris* were found in *Ceratophyllum demersum* collected from Diamond Pond but were not recovered from within the sediments.

The topmost macrofossil sample yielded a fish scale. Its ctenoid shape indicates that it came from a fish related to the sunfishes. The recently introduced largemouth bass has this type scale. In addition, 22 two- to three-millimeter-long, lunate-shaped objects, each with a hard enamel coating (perhaps teeth), were recovered from 9.1 to 8.7, 7.8 to 7.7, 4.0 to 3.8 m, and in particular from a unit with crumb structure from 6.9 to 6.6 m.

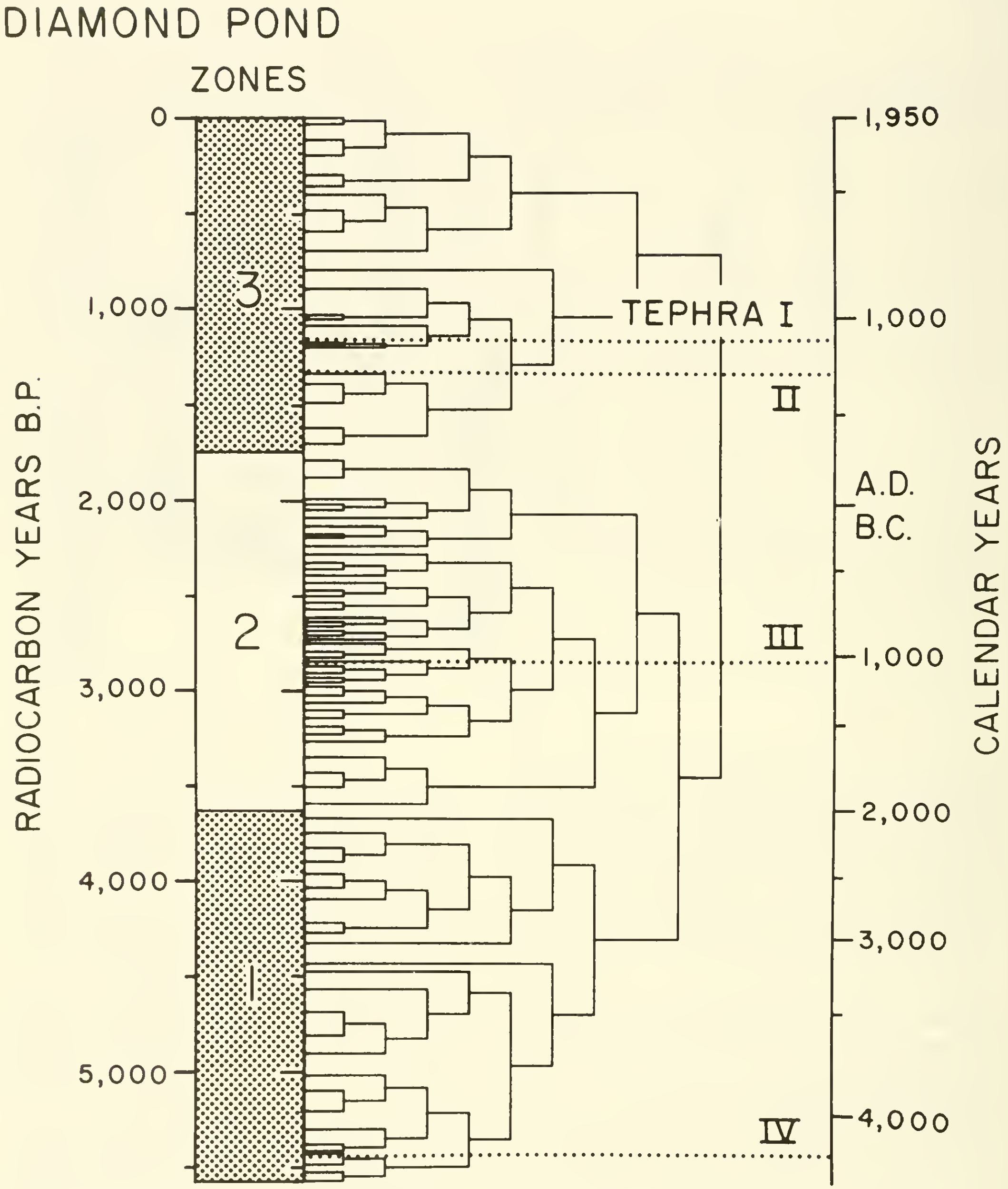

Fig. 15. Zoning diagram showing the clustering of adjacent pollen samples plotted by age.

Although numbers of plant macrofossils and mollusk shells vary dramatically from sample to sample, patterns of association and major trends are evident. Below 11.8 m (ca 5500 B.P.) plant macrofossils are absent; instead, some beds contain numerous aquatic insect parts. Especially abundant were members of the family Corixidae (water boatman), which feed on algae and other minute aquatic organisms.

In general, variation in plant macrofossil abundance suggests that submerged aquatic plants, emergent aquatic plants, and littoral plants respond as groups (Table 1). It appears that although changes in the numbers of submerged aquatic plant macrofossils may be out of phase with variations in the abundance of emergent aquatic plants, the species within each group fluctuate in concert.

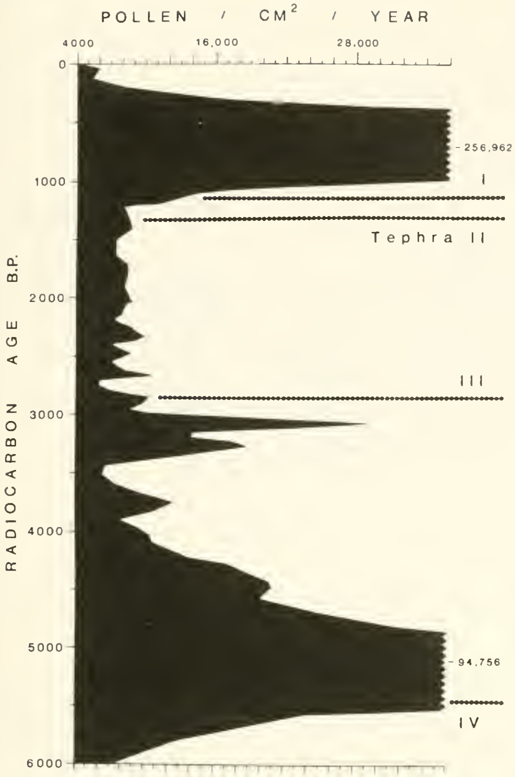

Fig. 16. Terrestrial pollen cm^{-2}/yr^{-1} plotted by radiocarbon age. Deposition rates were determined from the first derivative of a fourth order polynomial fit of radiocarbon ages with depth (Fig. 11).

Occasionally, both the seeds and pollen of certain plants occurred in Diamond Pond. To compare fluctuations in the abundance of the macrofossils of these species with changes in their corresponding pollen types, standardized macrofossil counts and pollen percentages as a percent of total pollen minus the six most abundant pollen types (*Artemisia*, *Sarcobatus*, *Juniperus*, Gramineae, *Pinus*, and other Chenopodiineae) were plotted (Figs. 18, 19).

Discussion

Interpretation of the Pollen and Seed Record

(Pollen, Macrofossils, and Ratios)

Both long- and short-term trends in the pollen and macrofossil records are evident (Figs. 14, 17). Long-term trends are characterized by two patterns, one that crosscuts zone boundaries and another that corresponds to zone boundaries. Whereas percentages of *Pinus* (pine), sagebrush, Cyperaceae, and other *Potamogeton* pollen have increased since 6200 B.P., pollen values of greasewood have declined. Ratios of pine, sagebrush, and greasewood emphasize these trends (Figs. 20, 21). The second long-term pattern is characterized by a pronounced increase in pollen values between about 3800 and 2000 B.P. Pollen percentages of other Chenopodiineae (although it also shows a general decline in pollen values since 6200 B.P.), grass, and juniper were all significantly larger at that time (Figs. 14, 20, 21).

Charcoal abundance with respect to pollen sum also increases between 3800 and 2000 B.P. (Fig. 22). According to the Pearson product-moment correlation coefficient, both sizes of charcoal are positively correlated ($r = 0.84069$, significant at $P = .0001$). Additional ratios of Charcoal A, Charcoal B, and total charcoal to each of the major types of pollen repeat the same pattern of charcoal abundance.

These long-term microfossil trends help characterize the pollen zones. Zone 1 is characterized by overwhelming abundance of greasewood pollen. Increasing percentages of sagebrush and relatively high percentages of juniper and grass and non-*Sarcobatus* Chenopodiineae pollen—probably *Atriplex* (saltbush)—are the hallmarks of Zone 2. In Zone 3 sagebrush pollen reaches its maximum abundance, whereas grass and juniper pollen percentages decline.

Short-term deviations of 100 or 200 years' duration interrupt the general trends outlined above (Fig. 13). Usually these variations are minor, but occasionally significant change in pollen contribution is evident. In general, increases in greasewood pollen percentages are out of phase with sagebrush, grass, and juniper pollen percentages. Although grass and juniper pollen values usually vary in the same direction, in Zone 3 they are often out of phase. Greater pine pollen percentages generally correspond with or immediately follow increases of juniper pollen percent.

Generally, the numbers of submerged, emergent, and littoral macrofossils generally have declined since about 5500 B.P. (Fig. 23). Dramatic fluctuations in their numbers do not necessarily correspond to changes in the ratio of aquatic (submerged plus emergent) to lit-

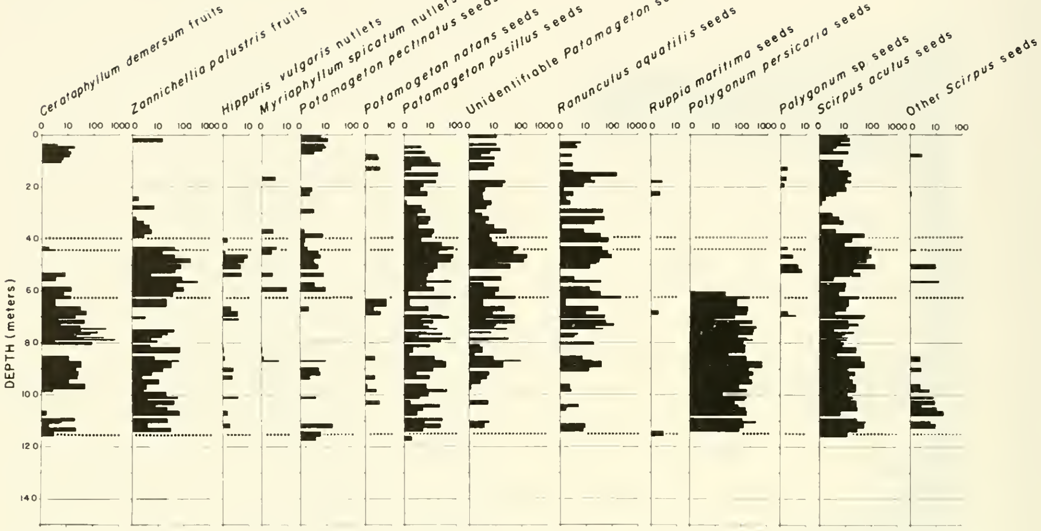

Fig. 17. Numbers of macrofossils recovered from Diamond Pond, standardized for 1,000 ml of sediment, are plotted on a log scale.

toral macrofossils. The ratios of both aquatic (*Potamogeton pectinatus*, other *Potamogeton*, *Polygonum persicaria*, and *Myriophyllum*) to littoral (Cyperaceae, *Typha*, and *Rumex*) plant pollen and aquatic to littoral plant macrofossils reveal dramatic short-term fluctuations in the abundance of aquatic and littoral plants (Figs. 21, 23).

MODERN POLLEN RAIN.—The surface pollen studies of Davis (1981:Appendix 16, 1984: Fig. 3) and Henry (1984) in southern Idaho offer modern pollen comparisons for the fossil pollen record from Diamond Pond. Although Davis's Albion Mountain surface pollen percentages do not "duplicate" environments of deposition in lakes and ponds, they provide several useful clues that help characterize past plant communities at Diamond Craters. These are:

1. *Juniperus* pollen in excess of 7% indicates that juniper was growing near or at the site.
2. *Sarcobatus* pollen in excess of 10% characterizes greasewood communities.
3. *Artemisia* values in excess of 50% characterize big sagebrush communities.
4. Other Chenopodiineae values in excess of 20% characterize shadscale communities.

Because Diamond Pond is located in the ecotone between the shadscale and lower sagebrush zones, aspects of both communities influence the pollen assemblage. Except for grass and juniper pollen percentages between 4000 and 2000 B.P., values of the major terrestrial pollen types at Diamond Pond have always been similar to those obtained from greasewood communities in the Albion Range (Davis 1984) and from the Terreton Basin of southeastern Idaho (Bright and Davis 1982). Grass and juniper pollen percentages from 3800 to 2100 B.P. and 1100 to 900 B.P. are comparable to those obtained from Davis's juniper and grassland communities, but the shadscale community pollen component is much stronger.

Comparison of modern and fossil pollen values suggests that plant communities that grew around Diamond Pond when juniper and grass pollen were most abundant have no modern analogue either in the Albion Range or at Diamond Pond. Fossil pollen evidence from Diamond Pond indicates that juniper and grass were part of the nearby shadscale community or that grass and juniper grew very close to greasewood- and saltbush-dominated areas. Juniper values of 8 to 12%, as well as radiocarbon-dated juniper from woodrat middens at Diamond Craters, indicate that juniper was growing in areas where it does not grow today (Mehringer and Wigand 1987, 1988). However, because the values of juniper pollen are on the low side of those

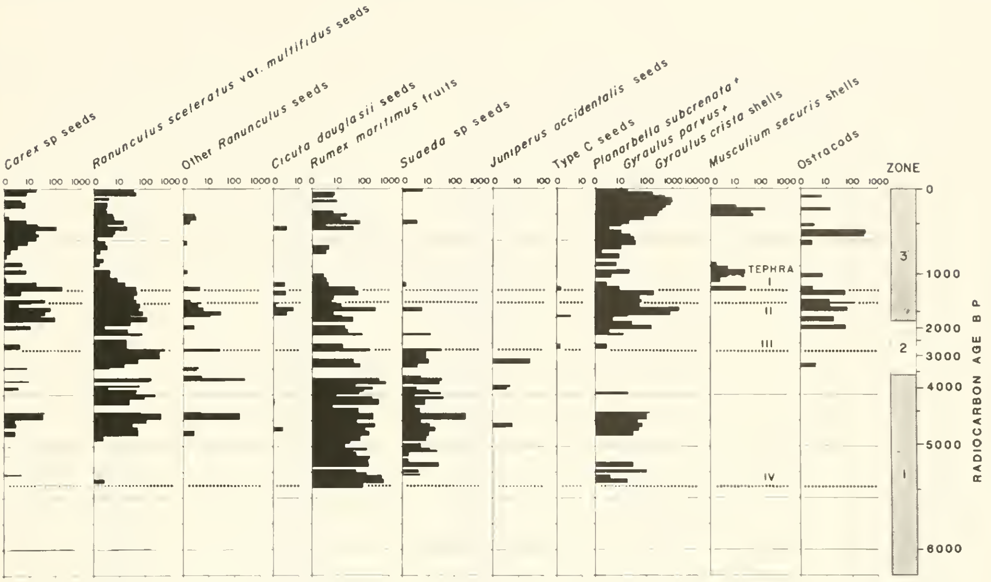

Fig. 17 continued.

expected for modern juniper zones, the trees probably were more dispersed.

JUNIPER, RAINFALL, STREAM DISCHARGE, AND WATERTABLE.—Juniper growth, together with its relationship to effective precipitation, is complex and beyond the scope of this study. However, there is evidence that winter rainfall may be critical in maintaining established juniper stands (Jeppesen 1978) and that the May/June rainfall component may also be important (Peter 1977:50–51). Between 1890 and 1910, 1940 and the early 1950s, when this rainfall component predominated, tree growth, as reflected in the tree-ring widths, was especially good (Peter 1977:Fig. 10). At the same time juniper stand establishment in northern California increased dramatically (Young and Evans 1981:Figs. 2, 3). One might conclude that in the past juniper expansion must also have reflected greater effective precipitation.

The historical correspondence of rainfall and increased stream discharge and higher lake levels in the Harney Basin is clear. Rainfall records for the Harney Basin indicate that dry decades reflect low winter and spring rainfall and are characterized by decreased runoff and shrinking lakes and marshes (Piper et al. 1939, Walker and Swanson 1968, Hubbard 1975). High winter and spring rainfall

TABLE 1. Aquatic and littoral species recovered from Diamond Pond.

Scientific name	Common name
Submerged Aquatic Species	
Ceratophyllum demersum	hornwort
Zannichellia palustris	horned pondweed
Hippuris vulgaris	common mare's-tail
Myriophyllum spicatum var. *exalbescens*	spiked water-milfoil
Emergent Aquatic Species	
Potamogeton pectinatus	sego pondweed
Potamogeton natans	broad-leaved pondweed
Potamogeton pusillus	small pondweed
Potamogeton other (broken *P. pusillus*?)	pondweed
Ranunculus aquatilis	white water-buttercup
Ruppia maritima	ditch grass
Polygonum persicaria	spotted smartweed
Polygonum sp.	smartweed
Littoral Species	
Scirpus acutus	hardstem bulrush
Carex sp.	sedge
Ranunculus sceleratus var. *multifidus*	celeryleaved crowfoot
Ranunculus sp.	buttercup
Cicuta douglasii	western water-hemlock
Rumex maritimus	golden dock
Terrestrial Species	
Juniperus occidentalis	western juniper
Atriplex confertifolia	spiny saltbush
Suaeda sp.	seablite
cf. *Lupinus* (Type C)	lupine
Liguliflorae	

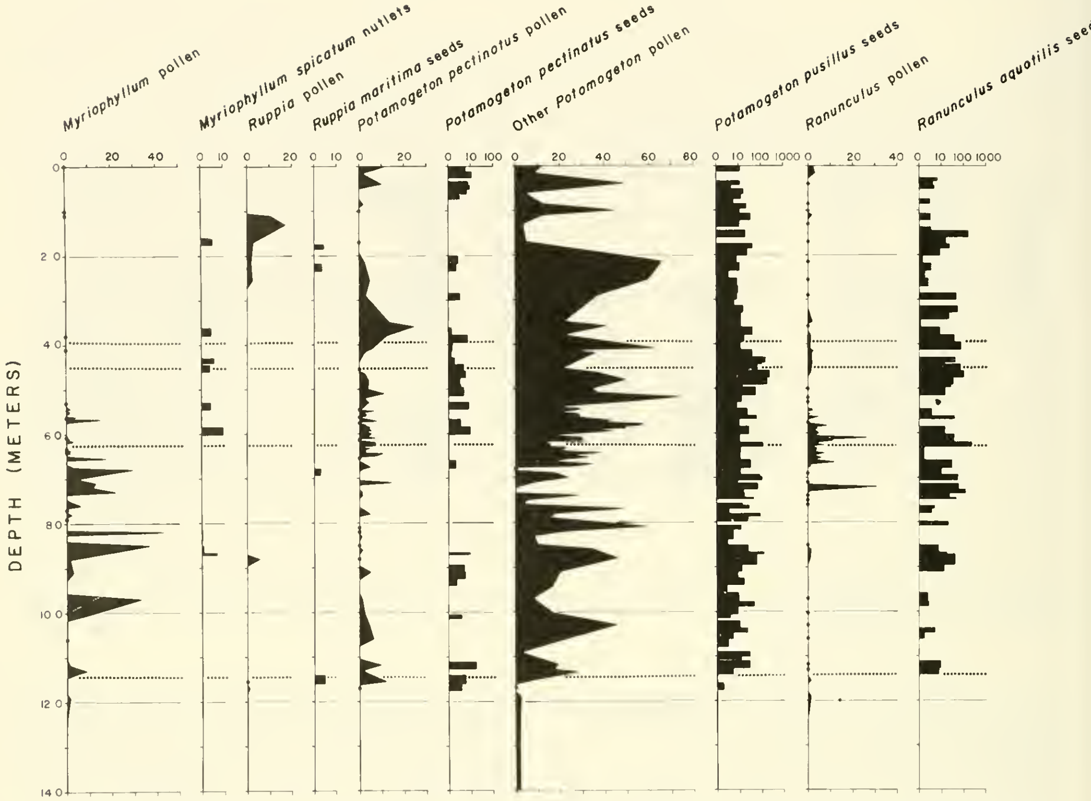

Fig. 18. A comparison of pollen percentages (percent of total pollen excluding the six most abundant terrestrial pollen types—*Artemisia*, Gramineae, *Sarcobatus*, *Pinus*, *Juniperus*, and other Chenopodiineae) and numbers of macrofossils (standardized to 1,000 ml of sediment; Fig. 17).

with increased runoff, and higher lake levels and expanded marshes characterize wet decades. This pattern has been aptly demonstrated during the last 10 years in the Harney Basin.

It is evident that juniper spread several times during the past 4000 years into areas where it does not grow today (Mehringer and Wigand 1987, 1988). If this was the result of increased precipitation, evidence for resulting higher water tables should be reflected in the water depth fluctuations indicated by the plant macrofossil record from Diamond Pond. Higher water tables should correspond with increased juniper pollen values.

Macrofossils and water table.—At Diamond Pond variation in assemblages of plant macrofossils can evidence changes in water depth resulting from (1) gradual or rapid infilling of the pond (reflected by the general succession from submerged to emergent aquatic plants to littoral plants), or (2) periodic water table fluctuations (reflected by rapid changes in the dominance of one group or the other that may or may not reverse the general trend from submerged aquatic to littoral species). If plant macrofossils were uniformly abundant throughout the deposits of Diamond Pond, a simple ratio of aquatic to littoral species should clearly reveal these variations. Deeper water would be reflected in greater abundance of submerged and emergent aquatic plant macrofossils at the expense of those from littoral species. However, the numbers of plant macrofossils vary greatly (Fig. 23).

The number of seeds or fruits deposited in pond sediments is dependent upon the number of seeds produced by the plant, how close it is to the place where the seeds are deposited, the plant's height, and whether or not its seeds can float (Birks and Mathewes 1978). Before 5500 B.P. absence of seeds in the sediments of the maar indicates that there was no vegetation growing in the pond. Since

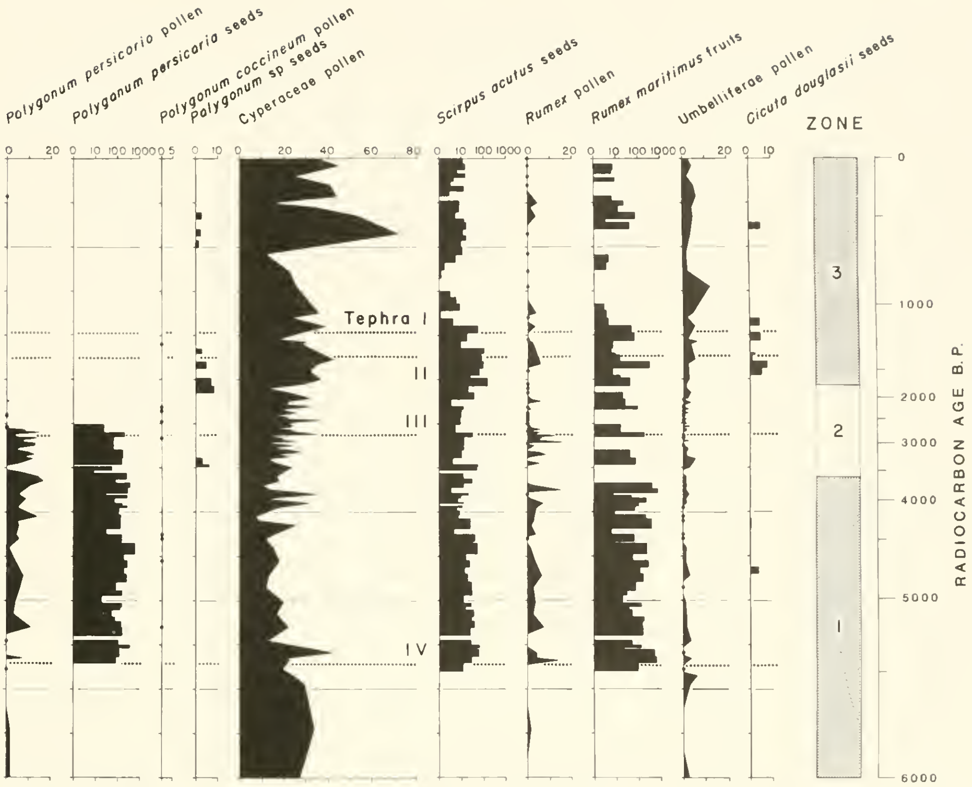

Fig. 18 continued.

the establishment of Diamond Pond, however, an uninterrupted pollen record indicates that it never dried out. Reduced numbers of macrofossils after 5500 B.P. could mean either that water depth in the pond had become so great that both aquatic and littoral plants had retreated to the margins of the maar and away from the center (the coring site), or that the species that were dominant could not disperse their seeds as well. Abundant plant macrofossils could mean the reverse.

As water depth increased, one would expect the number of seeds to decrease. However, the number of aquatic macrofossils would increase in proportion to littoral macrofossils not only because aquatic plants were closer to the center of the pond than littoral species, but also because there was more area for aquatic plant growth. As the water table dropped, one would expect greater macrofossil abundance and the proportion of littoral species should increase as they approached the center of the pond and reduced the area in which aquatic plants could grow.

Because at least 15 m of sediment has accumulated in Diamond Pond during the past 6000 years, the geomorphology of the maar probably has changed radically. The expected proportion of aquatic to littoral plants in a broad, shallow basin as Diamond Pond is today would have been quite different in the steep-sided, funnel-shaped maar of the past.

Because the diameter of the pond was smaller then, the center of the pond would always have been closer to all the plant communities in the maar even when water depth was great. Therefore, even though the general scenario described above would hold, the number of seeds would have been relatively much greater. Likens and Davis (1975) call this phenomenon 'focusing'. As the pond filled and became relatively much broader, one would expect the total number of macrofossils to decrease. This is what we observe

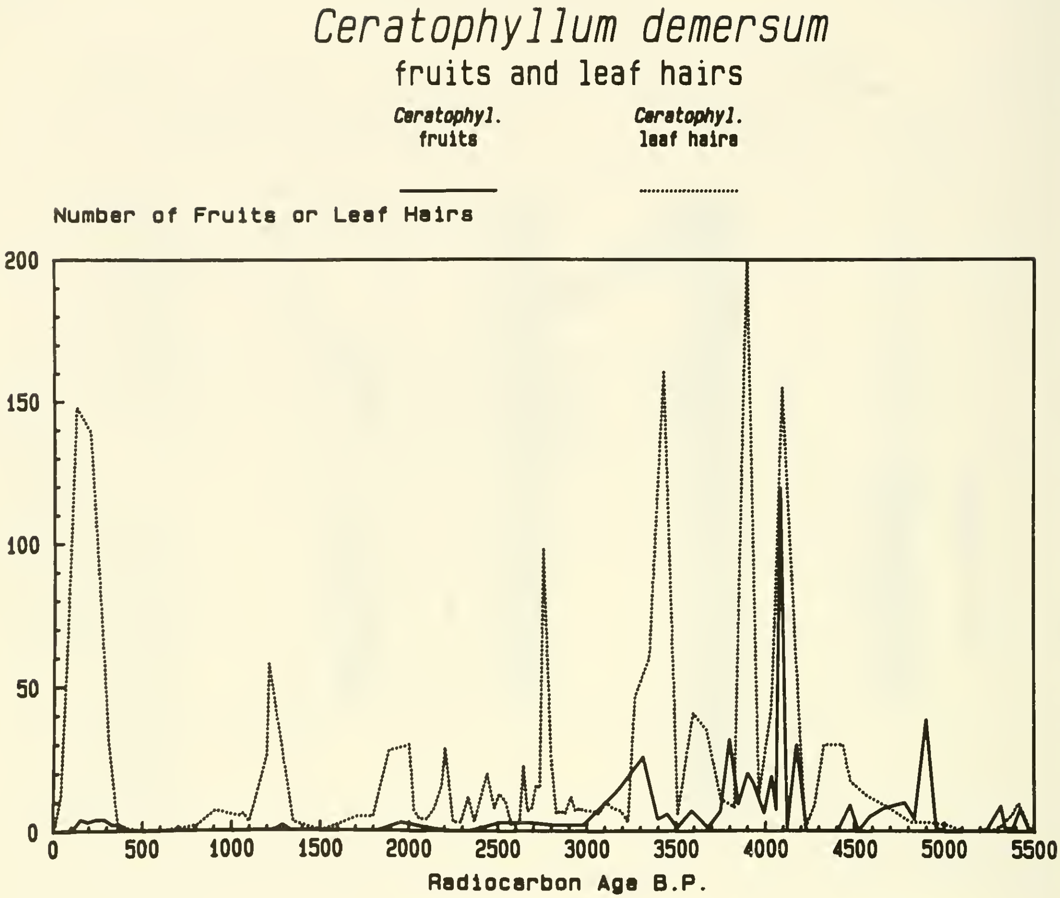

Fig. 19. A comparison of the number of *Ceratophyllum demersum* leaf hairs (expressed as percentage of the pollen sum) and the number of *Ceratophyllum demersum* seeds (standardized to 1,000 ml of sediment; Fig. 17).

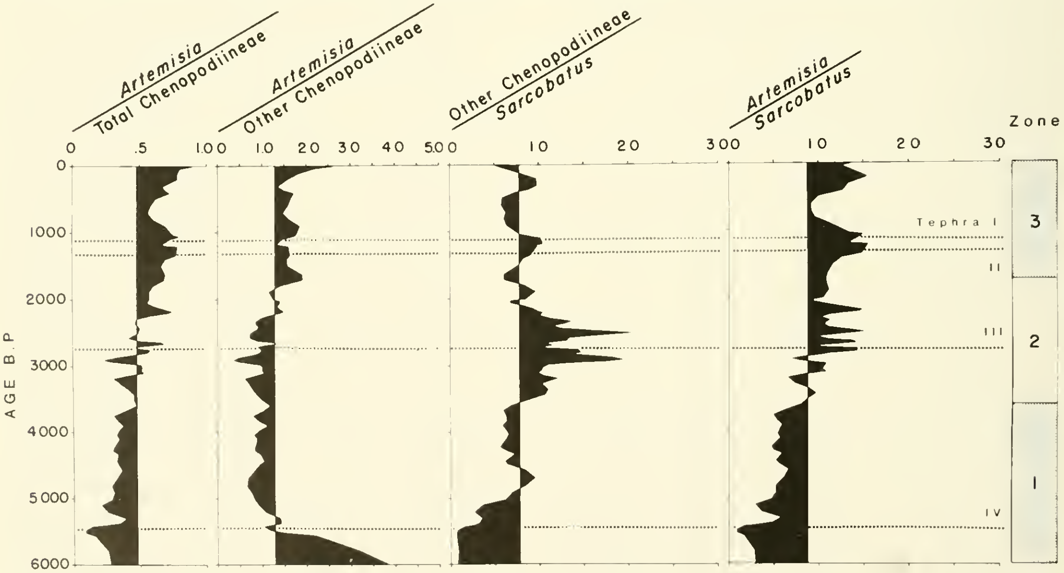

Fig. 20. Smoothed (a + 2b + c)/4 ratios of major pollen types, Part A.

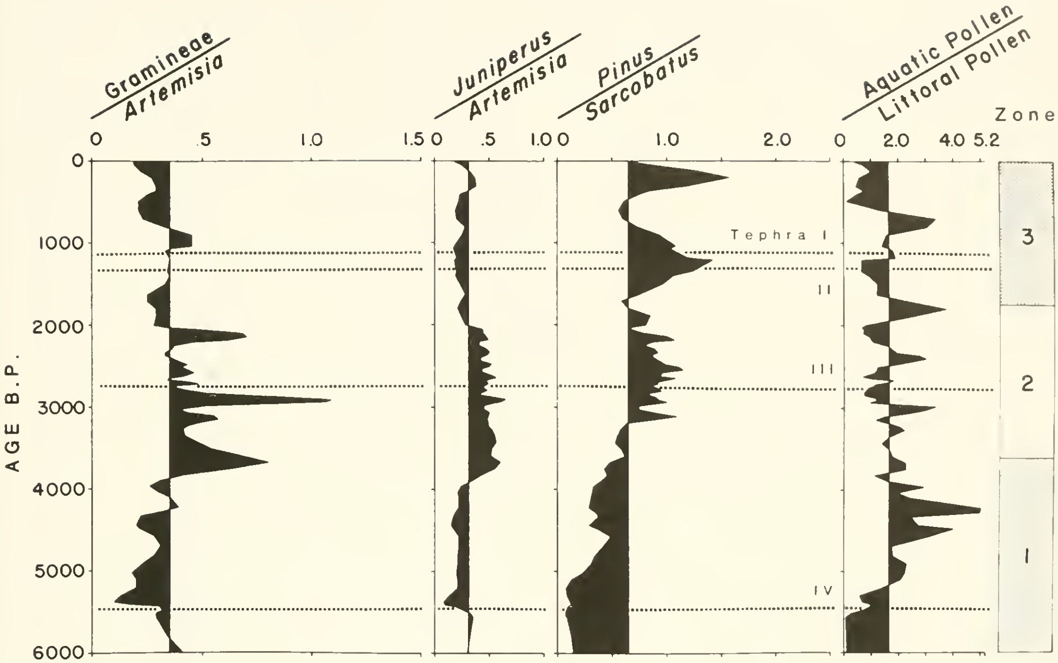

Fig. 21. Smoothed (a+2b+c)/4 ratios of major pollen types, Part B.

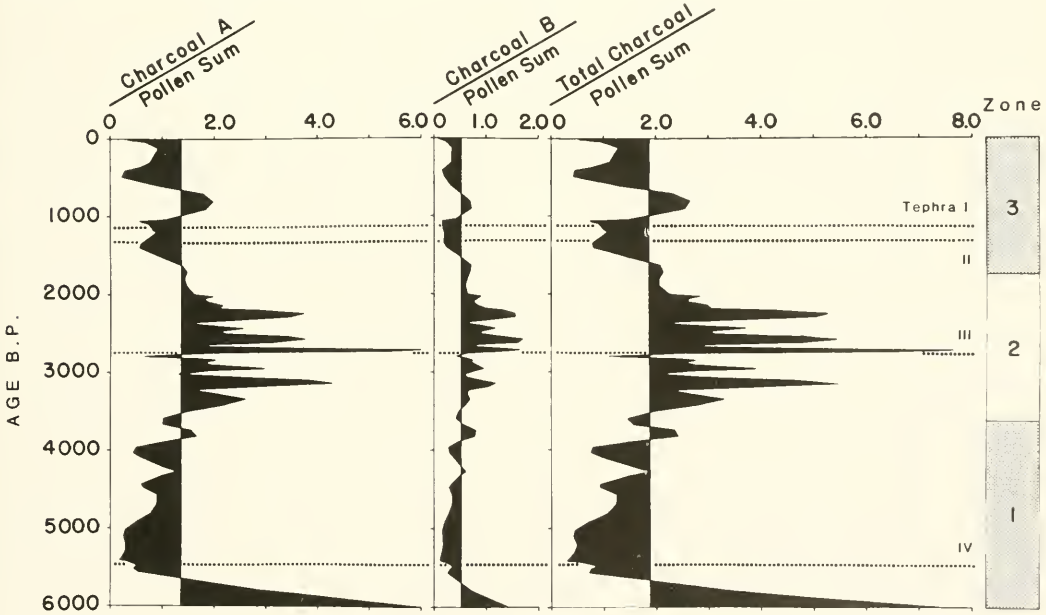

Fig. 22. Smoothed (a+2b+c)/4 ratios of total charcoal, Charcoal A (25–50 microns), and Charcoal B (> 50 microns), to the pollen sum.

(Fig. 23). However, the ratio of aquatic to littoral plants continues to reflect water depth as it did in the past. The fact that this ratio closely mirrors the juniper pollen percentage curve suggests that it does reflect the water table (Fig. 24).

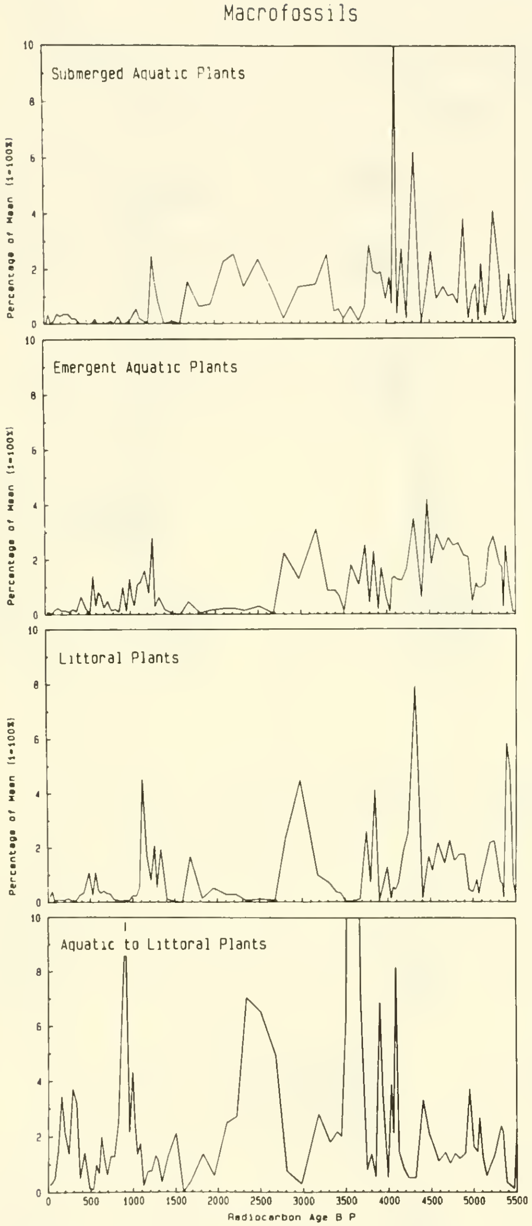

Fig. 23. Numbers of submerged, emergent, and littoral macrofossils expressed as percent of the 5500-year mean (1 = 100% on the scale). Ratio of aquatic (submerged and emergent) to littoral plant macrofossils (scale on the left is the proportion).

The Environmental Record

The record from Diamond Pond includes at least 6200 years, of which the period between 3600 and 2000 B.P. is revealed in detail unequaled in the northern Great Basin. Between 6000 and 5400 B.P. *Sarcobatus* (greasewood) pollen dominated the microfossil record. Its extreme abundance, up to 75% of the pollen sum, indicates that *Sarcobatus* (black greasewood) and other saltbushes, most likely *Atriplex confertifolia* (spiny saltbush) and *Atriplex spinosa* (spiny hopsage), covered the floor and lower slopes of Harney Basin. The preponderance of *Sarcobatus* pollen suggests that saline soils characterized the area (Branson et al. 1976).

The periodic occurrence of aquatic insects, algae, and finer sediments indicates that occasionally Malheur Maar supported ephemeral ponds. However, the absence of aquatic plant macrofossils suggests that the ponds were never permanent enough to maintain a growth of aquatic plants. The pond surface was seasonally at least 15–17 m below the present water surface of Diamond Pond. Because Diamond Pond acts as a standpipe for the local water table, such lowered water tables suggest that marshes in the Harney Basin were greatly reduced in area and probably dry for much of the year. Intermittent beds of sands accumulated in Diamond Pond from the periodic erosion of the sparsely vegetated slopes of Malheur Maar. Sands and coarse silts washed into Diamond Pond along with pollen (Figs. 12, 25). Concentration of pollen from the slopes of the maar in sediments of the ephemeral shallow ponds at its bottom resulted in abnormally high pollen accumulation rates, especially in Zone 1 (Fig. 16). Clay clasts in many of the beds indicate intense but sporadic rainfalls.

These data agree with the findings of others in the northern Great Basin concerning a dry mid-Holocene (Mehringer 1986, Davis 1982). On Steens Mountain at Fish Lake abundant sagebrush with respect to grass pollen between 8700 and 4700 B.P. reveals lower effective moisture than before or after, and sagebrush to grass ratios at Wildhorse Lake indicate warmer temperatures (Mehringer 1985:Fig. 12).

A dramatic and totally unparalleled increase (within the Diamond Pond record) of sagebrush pollen about 5300 B.P. indicates the first in a series of wet periods that herald the end of mid-Holocene drought. However, because this event follows closely the fall of the 5460 B.P. pumice, it is possible that the

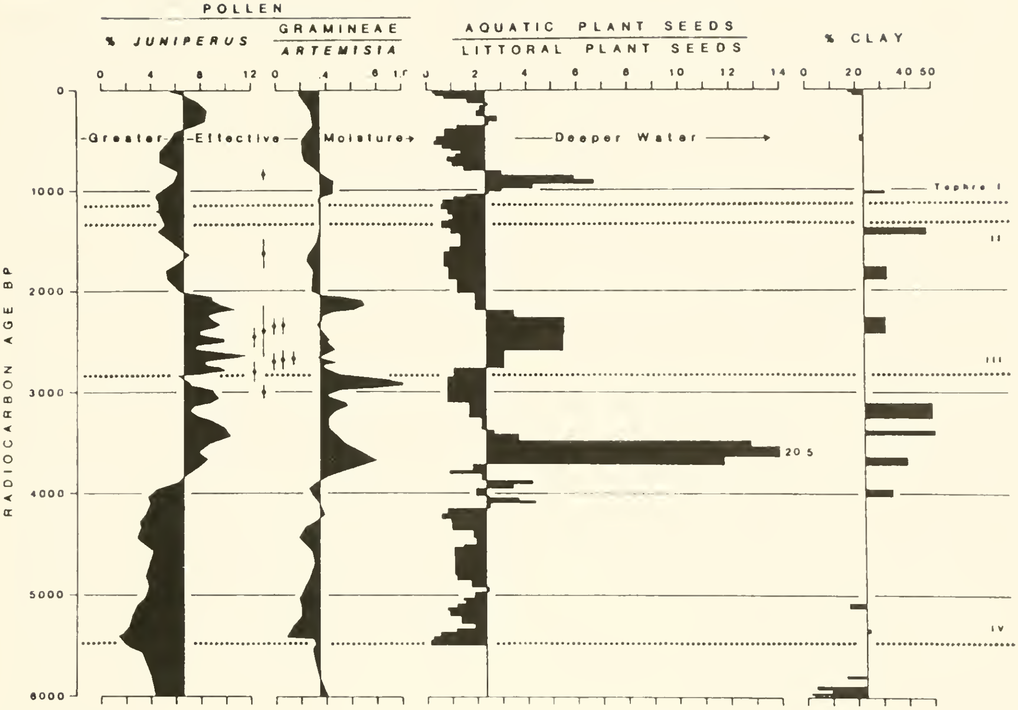

Fig. 24. Summary diagram including, from left to right: (1) smoothed juniper pollen percentage, (2) radiocarbon dates on juniper macrofossils from packrat middens, (3) smoothed ratio of grass to sagebrush pollen, (4) ratio of aquatic to littoral plant macrofossils, (5) percent of clay per sediment sample.

pumice, by acting as a mulch, may have contributed to the spread of sagebrush. On the other hand, because the increase was short-lived, with greasewood soon the dominant plant again, it is more likely that a brief interval of greater effective moisture was the cause. By 5000 B.P. greasewood was in full retreat before the advance of other saltbushes, sagebrush, and grass. They continued their slow spread at the expense of greasewood until ca 3800 B.P.

The appearance and sudden abundance of littoral and aquatic plant macrofossils and mollusk shells shortly before the fall of Tephra IV (5460 B.P.) indicate that Malheur Maar contained a relatively permanent body of water with lush aquatic growth. A marsh dominated by *Scirpus acutus* (hard-stem bulrush) and *Rumex maritimus* (seaside dock) was quickly replaced by a permanent pond filled with a variety of aquatic plants, primarily *Ceratophyllum demersum* (hornwort), *Polygonum persicaria* (spotted smartweed), *Zannichellia palustris* (horned pondweed), and *Potamogeton pusillus* (small pondweed), and surrounded by a littoral community still dominated by bulrush and dock.

By 4400 B.P. the water table was within 10 m of its present level. Rising water table at Diamond Pond suggests that mid-Holocene drought had given way to effectively moister conditions. Resultant higher regional water tables would enable the Malheur Marshes to expand into areas formerly occupied by greasewood. This, together with the invasion of other saltbush and sagebrush communities into the upper reaches of greasewood-dominated areas, may explain the sudden drop in *Sarcobatus* pollen values.

Between 3750 and 2050 B.P. increased grass and juniper pollen values reflect the spread of juniper and grass into sagebrush and shadscale communities around Diamond Pond (Fig. 24; Mehringer and Wigand 1987, 1988). Charcoal proportions greater than before or after this period may evidence more frequent fires resulting from more abundant fuel. Low greasewood pollen values reflect the continued presence of marshes and saltbush and sagebrush communities in areas pre-

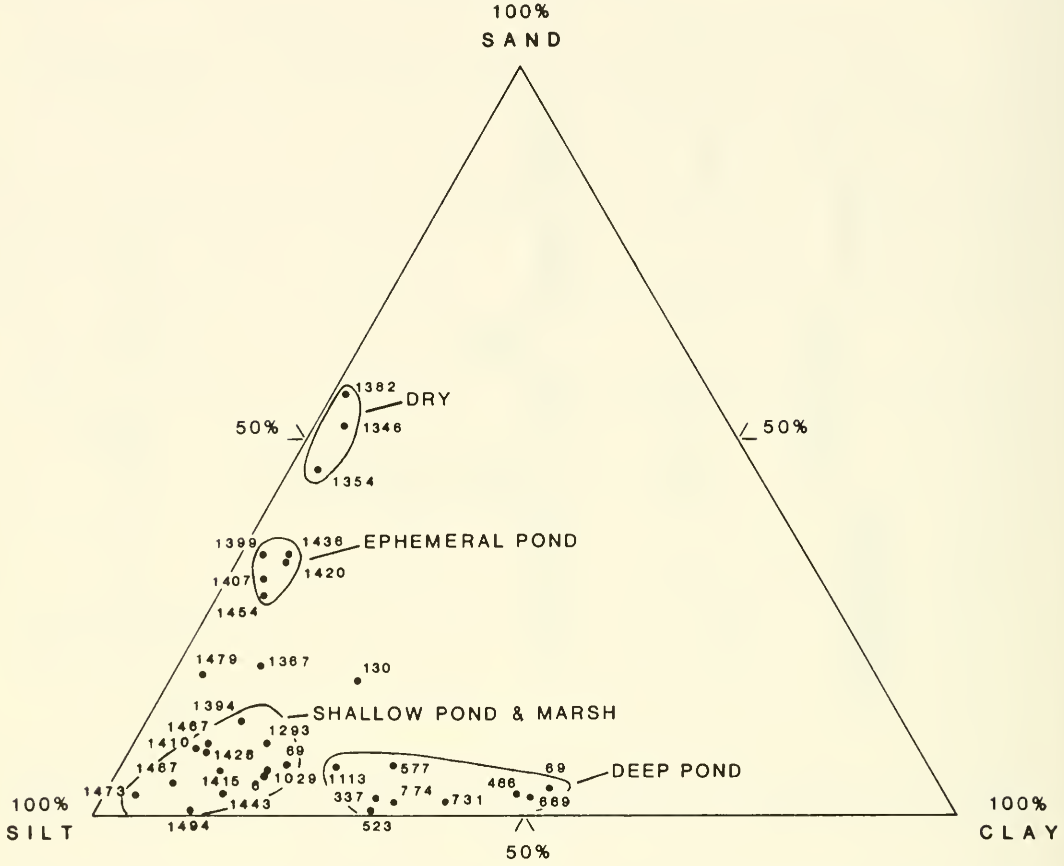

Fig. 25. Proportions of sand, silt, and clay in Diamond Pond sediments and their relationships to water depth as suggested by plant fossils. Numbers indicate sediment depth in centimeters (Fig. 12).

viously occupied by greasewood. From 3800 to 3600 B.P. high juniper and grass pollen values, also reflected in the pollen ratios, correspond to the greatest abundance of submerged and floating aquatic plants as compared to littoral species. The water table may have risen more quickly than the accumulation of sediment in Diamond Pond to make it deeper than at any other time. Proportions of clay in excess of 25% also suggest deep water (Figs. 12, 25).

Throughout the Great Basin, rising lake levels and changing plant communities evidence alleviation of the mid-Holocene warm period (Mehringer 1986, Davis 1982). Intensive human occupation of Hidden (Thomas et al. 1985) and Krammer (Hattori 1982) caves between 3800 and 3600 B.P., with corresponding extensive use of marsh plants and animals, indicates that marshes had reappeared near these sites.

Abundant rockfall in pond sediments of this period, especially after ca 3200 B.P., may reflect accelerated freeze/thaw activity resulting from colder temperatures or greater effective moisture. Because these rocks are found enclosed in fine sediment near the center of the pond, it is possible that they fell onto ice when the pond was frozen and were dropped when the ice melted.

Shortly before the fall of the 2845 B.P. volcanic ash (Tephra III), finely laminated pond deposits are interrupted by a unit of crumb structure with numerous salt crystals and the largest carbonate percentage in the Diamond Pond record. A corresponding sharp increase of greasewood pollen values, decreased aquatic plant macrofossils, but more abundant littoral plant macrofossils support the suggestion of a brief but significant drought.

Except during this drought, submerged and floating aquatic plants dominate the macrofossil record between 4000 and 2000 B.P. and indicate at least five periods of deeper water (Figs. 23, 24). Following the pre-Tephra IV drought, several aquatic species either disappeared (*Polygonum persicaria*) or became more rare (*Ceratophyllum demersum*). Less-abundant floating and submerged aquatic plants after 2600 B.P. reflect the transition to a shallower pond due both to sediment accumulation in the maar and drier conditions. After ca 2050 B.P. both the sharp decline of floating and submerged aquatic plant macrofossils with respect to macrofossils of littoral plant and the dramatic fall of juniper and grass pollen values probably reflect a drop in the water table due to drier conditions.

Following 2000 B.P. declining juniper and grass pollen values may reflect their retreat to the higher northern parts of Diamond Craters where water perched in the shallow soils overlying the basalt flows and a north-facing aspect favored their survival. The sagebrush understory replaced them as the dominant vegetation. Increased values of juniper and grass pollen indicate expansion of grass and juniper ca 1600 B.P., between ca 1400 B.P. and 700 B.P., and between ca 450 and 200 B.P. Abundant grass characterizes the period between ca 1400 and 700 B.P., while juniper has only a brief increase about 900 B.P. Harper and Alder (1970, 1972) record a significant moist interval between 1500 and 600 B.P. Kelso (1970) inferred, from pollen data, a moist period dominated by grass beginning about 1500 B.P.

Dominance of littoral plant macrofossils in Diamond Pond indicates that water levels remained low through the first part of this period. About 900 to 800 B.P. more abundant submerged and floating aquatic plant macrofossils and greater juniper pollen percentages evidence effectively moister conditions. Greater proportions of clay in the pond sediments also suggest deep water ca 1400 and again ca 1000 B.P. (Figs. 12, 25).

After 700 B.P. at least two major droughts, one about 700 and another about 500 B.P., are indicated by increased values of greasewood. The occurrence of *Ruppia* pollen and seeds and the appearance of the fingernail clam, *Musculium securis*, indicate that Diamond Pond was more saline and dried out periodically. Analysis of at least one sample from this period showed sediments higher in sand than other sediments from Zone 3 (Figs. 12, 25). In addition, pollen accumulation rates between 800 and 450 B.P. (Fig. 16) are abnormally high. Both factors suggest decreased vegetation cover and increased erosion of the slopes of Malheur Maar.

Greater values of grass and juniper pollen about 300 B.P. indicate a return to effectively wetter conditions. This is supported by finer sediment, indicating deeper water (Figs. 12, 25), and by increased submerged and floating aquatic plant macrofossils, especially *Ceratophyllum demersum* (Fig. 19). Aquatic plant abundance is further supported by the presence of large numbers of *Planorbella* and *Gyraulus* snails, which favor thick aquatic vegetation. Recently, more abundant sagebrush pollen and declining juniper and grass values may result from a combination of fire suppression, water diversion, overgrazing, and logging, as well as changing climate.

Despite the accumulation of at least 15 m of sediment during the past 6000 years, a rising water table has maintained the pond. However, the trend from aquatic to littoral plant dominance reflects the long-term filling of Diamond Pond that will eventually terminate its existence.

CONCLUSION

The detail available in the pollen and macrofossil records from Diamond Pond, especially between 4000 and 2000 B.P., has allowed resolution of major climatic episodes lasting only one or two centuries with transitions of less than 25 to 40 years (Fig. 24).

Relative pollen frequencies from Diamond Pond mirror the response of dominant plant species of the local and regional plant communities to long- and short-term climatic change since the mid-Holocene. Aquatic and littoral plant macrofossils record details of fluctuating water depth of Diamond Pond, as well as the long-term infilling of Diamond Pond. Because aquatic and littoral plants spread and mature rapidly, they are sensitive indicators of changing effective moisture.

If the aquatic to littoral plant macrofossil ratio is an accurate indication of fluctuating water table and, by extension, expansion of the Malheur marshes, it seems that they were most extensive between ca 3750 and 3450 B.P. From ca 2800 to 2050, 1000 to 800, and

300 to 150 B.P., more abundant aquatic plant macrofossils indicate recharged local water table and marsh reexpansion. Major littoral plant increases about 2900 and 500 B.P. indicate severe drought.

ACKNOWLEDGMENTS

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COMPARISON OF HABITAT ATTRIBUTES AT SITES OF STABLE AND DECLINING LONG-BILLED CURLEW POPULATIONS

Jean F. Cochran[1] and Stanley H. Anderson[1]

ABSTRACT.—Long-billed curlew populations were studied in the upper Green River Basin of Wyoming. Sites were selected where curlew populations appear constant in numbers and declining in numbers. Results show that while few habitat differences were found between the two areas, disturbances such as grazing and dragging during nesting reduced productivity. Nest failures were also correlated with field fertilization and early season grazing. Within each area curlews nested successfully on field sites that were elevated and had adequate grass cover but not tall grass.

Before 1870 long-billed curlews (*Numenius americanus*) nested in relatively high numbers on prairielike habitats across North America (Audubon 1960, Palmer 1967, Johnsgard 1981). However, extensive hunting virtually exterminated the species from the eastern United States in the last third of the nineteenth century (Bent 1962). Their numbers continued to decline across the continent during the first 30 years of this century (Bent 1962). In addition to market hunting, many authors have cited plowing and heavy grazing of nesting habitat as causes for this decline (Oberholser 1918, Wolfe 1931, Sugden 1933, Yocum 1956, Johnsgard 1981).

During the 1930s, hunting pressure was reduced and efforts were made to reduce grassland grazing pressure on curlew populations (Yocum 1956). Long-billed curlews might have explored newly created "artificial" habitat (annual grasslands and irrigated lands) while native prairies were destroyed during that time period (Pampush 1980, Bicak et al. 1982).

Long-billed curlews have four essential nesting habitat requirements in the northwestern United States: (1) short grass (less than 30 cm tall), (2) bare ground components, (3) shade, and (4) abundant vertebrate prey (Pampush 1980). Bicak et al. (1982) and Allen (1980) presumed that a preference for large, open vistas and unobstructed forage dictated a need for short vegetation profile. An association with moist sites or water access has been documented (King 1978), but nests have also been found far from water and in generally arid sites (Bicak et al. 1982).

Our objective was to compare habitat characteristics and land-use activities between areas with stable and declining numbers of long-billed curlews to determine if habitat factors could be responsible for declines.

STUDY AREAS

Two study sites were selected in the upper Green River Basin of Wyoming. The Horse Creek site is eight miles west of Daniel near State Highway 354. This two-mile-long area is south of Myrna and Highway 354 and is bounded on the south and west by Horse Creek and Bridger National Forest. Sagebrush (*Artemisia tridentata*) and aspen (*Populus tremuloides*) cover the ridges and also encircle the flats except on the eastern outlet. This 3,000-ha area slopes from 2,315-m elevation in the west to 2,270 m in the east.

The second site, the New Fork study area, is located between Cora and Pinedale. The 2,000-ha New Fork site is bounded on three sides by sagebrush-covered hills. The elevation drops 8.7 m per km from 2,225 m in the north to 2,190 m in the south.

The climate of the upper Green River Basin is classified as continental steppe (Brown 1980). Annual precipitation ranges from 24 to 40 cm per year with 27–62% falling between April and September. Snow falls regularly from September to May, and heavy mountain accumulations provide summer irrigation water. Summers are short and cool, with the average growing season being 70 to 80 days (U.S. Department of Agriculture 1978).

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The vegetation in the upper Green River is principally sagebrush, with willow (*Salix* spp.) and sedge (*Carex* spp.) dominating sloughs in the weathered sites (Vale 1975). These sagebrush flats were converted to flood-irrigated hay meadows from the time of the first homesteads in 1892 to as late as 1960. After brush removal, some meadows were hand-seeded with timothy (*Phleum pratense*) and redtop (*Agrostis palustris*), while others were left in native graminoids. By the 1940s alsike clover (*Trifolium hybridium*) and reeds canary grass (*Phalarius arundinaceae*) had replaced redtop in mixed plantings with timothy.

Native plants have reinvaded many of the fields. The dominant invaders include wire grass (*Juncus balticus*) and some rush and mountain timothy (*Phleum alpinum*) (Hitchcock 1921). Many cultivated meadows are the result of conversion, beginning around 1960. These fields are thoroughly plowed, leveled, and then seeded with timothy, alsike clover, milkvetch (*Astragalus* spp.), meadow foxtail (*Alopecurus pratensis*), alfalfa (*Medicago sativa*), and other grasses. Cultivated meadows are fertilized annually with nitrogen or ammonium nitrate. In the 1970s some native meadows were also fertilized, but this activity has declined markedly since 1978 because of high costs. Approximately 90% of the total hectarage at Horse Creek and 83% at New Fork are hay meadows. The percentage of potential long-billed curlew nesting habitat is thus very similar at the two sites.

Sheep, cows, and hogs have been raised historically on both study sites, but current livestock are entirely beef cattle. From November to May cattle are confined to feed grounds near four ranches on Horse Creek Flat. After calving in April, herds are gradually shifted through a series of fields beginning in mid-May or June. Some fields in this flat are used solely for summer pasture. Many of the summer-pastured cattle come from other wintering grounds near the North Fork study site. The remaining cattle are moved to summer range off the flat. Hay is cut (once annually) from nonsummer-pastured fields starting at the end of July and continuing through August or September.

Meadow dragging is a land-use practice which affects ground-nesting birds. This is done in the spring to break up manure piles left by fall- and winter-pastured cattle. Drags can be anything from tree branches or scrap metal tied behind a large log to modern harrows. Dragging has declined since the mid-1960s because of fuel and labor costs and a decrease in haying.

Both sites are irrigated. At New Fork, water flow is regulated by a large upstream dam. Spring irrigation water is not released until 1–10 June, leaving fields dry in May. The water is shut off for 7–10 days before haying. Horse Creek has not been dammed. Fields are flooded as soon as the snow melts (usually mid-May), and water continues to saturate the meadows until mid-July in most years. Both areas are underlain by gravel beds up to 9 m deep. These beds fill with water so that the hay crops are irrigated constantly from below, in addition to surface flow.

METHODS

Preliminary observations were made in May–August 1981. During this time we became familiar with principal use areas and behavior patterns of curlews. Field sites were then selected. Field data were collected 5 May–20 August 1982.

POPULATION INDICES.—Long-billed curlews were counted 5 May–19 July 1981 and 1982 using roadside surveys on prescribed routes in each study area. A modified version of the Breeding Bird Survey (Robbins et al. 1986) was used to sample the greatest number of birds over a greater distance. Survey results were converted to number of birds seen per kilometer of road surveyed. Twenty-two surveys were completed at Horse Creek and 18 at New Fork in 1982. Curlew locations by sex were marked on a 1:24,000 topographic map. Long-billed curlews were sexed by bill length (Allen 1980).

HABITAT DATA.—Native and cultivated fields were sampled at both study areas. Timing and level of grazing pressure based on numbers of cattle were recorded so that comparisons could be made with curlew use. Each of the 65 hay fields was divided into four 200-m-wide strips, and parallel transects were run down the center of each strip. Preselected random points were located by pacing along transects with only one point per 80-m interval. Thus, one random point was selected from each 200 × 80-m block of the field.

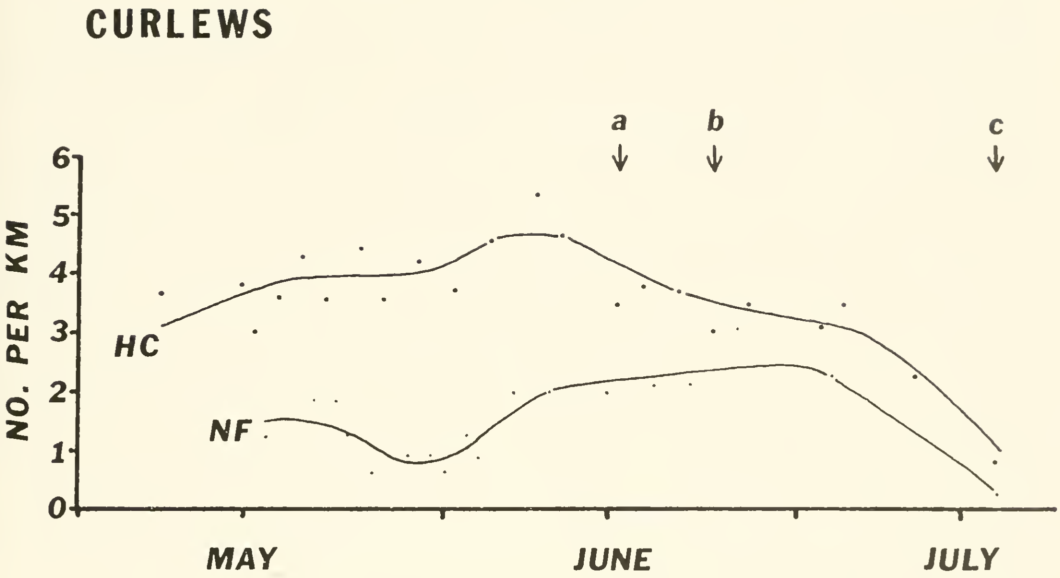

Fig. 1. Number of long-billed curlews seen per kilometer surveyed, 5 May–19 July 1982; a = date of first hatch at Horse Creek, b = hatch at New Fork, c = last hatch at Horse Creek.

Specific habitat variables were measured as follows: visual obstruction or "effective height" (Robel et al. 1970) of hay was estimated against a 5-cm-diameter Robel pole marked with alternating black and white 2.5-cm bands. Measurements were taken 1.5 m away from the pole and aligned with the east-west or north-south transect. The approximate eye level for curlews is 30 cm above the ground (Redmond et al. 1981). This was mimicked by kneeling until the observer's eyes were even with a 30-cm-tall stick. The lowest 2.5-cm band visible on the Robel pole from this vantage point was then recorded as the effective height.

From the same position, the within-meadow microtopography was estimated visually by comparing the height of the ground at a random point to the ground 5 m beyond (Skeel 1976). If the sample point was approximately 2.5 cm above the surrounding ground, or less, it was classed as level. Drops of 2.5 cm or more below the background usually represented the canal or swale. Small, medium, and large hummocks were defined as sample points 2–10, 11–20, and greater than 20 cm above the surrounding ground.

Vegetation and bare ground cover were placed in one of seven cover classes with the aid of a 20 × 50-cm Daubenmier frame (Daubenmier 1959). These classes of cover were grasses, sedges, rushes, forbs, mosses, bare ground, and litter. Soil moisture measurements were grouped into three categories for analysis: (1) wet, or standing water, (2) damp, and (3) dry. In May the distance to the nearest cow manure pile greater than 2.5 cm in diameter was measured with the Robel pole.

Field boundaries and size of vegetation communities were estimated from aerial photos. Land-use data were determined from aerial photos and verified in the field. Interviews with ranchers indicated dates of dragging, fertilizing, and flooding as well as cattle movement.

NESTING HABITAT.—Nest searches were concentrated in fields where male curlews had been observed displaying in 1983 (Allen 1980). Defensive and disturbed birds were also used as clues for finding nests. Once nests were located, habitat information was collected after chicks had hatched. The following data were collected: horizontal cover by grass or sedge, rushes, forbs, and bare ground around the nest; height of nest; distance from nest to nearest canal, road, building, willow bushes, and manure pile; hay field type; and material used in nest construction. Nesting habitat was then analyzed in four ways. First, a group of 18 nests was compared randomly to available habitat and hay meadows. Second, comparisons were made between individual nests and habitat data from the fields in which they were located. Third, comparisons were made between successful and failed nest sites. Comparisons were also made between nest fields and non-nest or avoided fields.

Starting in June, nests were monitored through hatching. Every three to seven days the incubating bird was flushed so that eggs could be checked for signs of hatching. Otherwise, nests were observed from a distance of 10 to 100 m to confirm the presence of an incubating curlew. Disturbance to nesting birds was minimized by walking directly to the nest from the same direction and staying within the nest field or site of the curlew as briefly as possible. A few paradichlorobenzene crystals were scattered after the observer's trail to discourage scent-tracking predators (Redmond 1986). Flushing distance, distraction-display response to other birds, and time of day were noted on each visit.

DATA ANALYSIS.—Data were analyzed with SPSS Batch System: Statistical Packages for the Social Sciences (Nie et al. 1975). The programs used were BREAKDOWN, FREQUENCY, T-TEST, ONE-WAY (analysis of variance or AOV; stepwise and multiple) REGRESSION. All analyses of variance were one-way, and all t-tests were unpaired or unpooled. Differences between means are considered significant if probabilities were less than .05.

RESULTS

POPULATION INDICES.—Roadside counts of curlews showed significantly more birds per kilometer of road at Horse Creek, where curlew numbers increased until 10 June and then declined to 18 July. New Fork counts showed more variation but were consistently lower than Horse Creek. The highest count of birds was 4.06/km at Horse Creek and 1.45/km at New Fork (Fig. 1).

HABITAT COMPARISONS.—No vegetation differences were apparent from May surveys between cultivated and native field types. Spring grazing had repressed vegetation height to a mean of 2.38 cm in June. Ungrazed native fields averaged 4.78–5.63 cm, and cultivated hays had grown from 7.88 to 9.88 cm. Further, spring-pastured meadows were significantly shorter than both hayed only and fall-pastured meadows (all probabilities are significant if less than .05).

When all land-use types were pooled, no significant differences in vegetation height were detected between New Fork and Horse Creek in either May or June. When various types were considered separately, minor differences arose. Native hayed, pastured fields were shorter at Horse Creek than at New Fork in May (1.25 vs. 1.48 cm). Again in June, a difference between native fields at the two study sites was found. Only cultivated hay samples were consistently taller in June at Horse Creek than New Fork. Thus, vegetation height or visual obstruction differed between land-use types in the growing season (June).

Coverage by grasses, sedges, rushes, and bare ground differed between cultivated and native fields but not between study sites. Overall, ground cover in native fields averaged 24.4% grasses, 23.6% sedges, 22.7% bare ground, 9.9% rushes, 7.8% forbs, and 0.8% mosses (10.9% was unaccounted for because cover classes included a 0% but not 100%). In cultivated fields, ground coverage averaged 68.7% grasses, 10.1% forbs, 9.3% bare ground, 1.9% sedges, 0.8% rushes, and 0.4% mosses. Thus, native fields were covered by approximately equal quarters of grasses, sedges, bare ground, and all other plants, while cultivated fields were at least three-quarters grasses and about one-tenth each forbs and bare ground. Despite the planting of clover in cultivated fields, these meadows did not average significantly more forb coverage than did native fields. Coverage by grasses was significantly greater in cultivated hay fields but did not differ between study sites.

The average ground height was not significantly different in cultivated, native Horse Creek or New Fork fields. However, average height may not convey the relative "bumpiness" of fields. In casual observation, some native fields contained numerous hummocks, but all cultivated fields had been leveled.

All meadows were significantly wetter in June than May due to irrigation, but Horse Creek had even more wet ground than New

Fork when both were irrigated. Horse Creek was also significantly wetter than New Fork in May when these sites were compared. Pooled samples (May plus June) showed that Horse Creek meadows were wetter than New Fork meadows.

NESTING SUCCESS.—At Horse Creek, curlews hatched from 15 June to 12 July 1982. The one hatch seen at New Fork occurred on 24 June. The second New Fork clutch had hatched by 20 June when we visited the nest, and the third brood seen there was probably one to two weeks old on 24 June. Thus, mean hatch date on Horse Creek was 1 July, and New Fork mean hatch was 24 June.

We observed 21 long-billed curlew nests in 1982. Of the 21 nests, 3 were in cultivated hay, 1 in an unmowed slough, and 1 in an overgrazed, dry pasture. The remaining 16 curlew pairs nested in subirrigated, native hay meadows that were mowed annually. Three of these were in fields that were never pastured.

Using the Mayfield (1961, 1975) method, which compensates for unknown nest-initiation dates of failed nests, we calculated an overall nest-survival rate of 33.6%. Forty-four percent of the young survived from all Horse Creek nests, while 28.3% of non–Horse Creek nests lived. Clutch size was 3.83 with an incubation period of 28 days. Redmond and Jenni (1986) found similar results in Idaho with most females laying four eggs and incubating 28 days.

NESTING HABITAT.—Grass cover immediately around 18 nests was almost double the grass in fields generally. Nests were built in sites with less bare ground than the fields overall. Where the ground had not been leveled (native fields), nests were found on sites significantly higher than mean level ground. Average height at nest sites was 6.1 cm above the ground in a radius of 1–5 m around the nest. These heights were classed as either small hummocks or level ground. Six of the 15 nests were on hummocks (at least 2.5 cm above surrounding ground). Two of these were higher than 20 cm, while only 2 out of 320 randomly sample points were that high. Chicks hatched successfully from 5 of the 6 hummock nests (the sixth was destroyed by dragging), but 6 of the 9 level nests failed. No nests were on depressed ground (less than 2.5 cm below the surrounding ground).

Nests were found in fields that had significantly less bare ground than did the randomly sampled fields. Nests built where cattle had pastured were directly against a manure pile. Clearly, these nests were closer to conspicuous objects than could be expected from random placement.

When hatching success for 21 nests was regressed on conditions surrounding the nests, two land uses were found that predicted nest failure: grazing during incubation, and field fertilization. Nest field dragging, nest flooding, and nest height did not correlate with nest failure.

The last measure of nest habitat selection was the comparison of fields used for nesting and those not used. Three habitat traits were significantly different between these fields: percent cover by grasses, percent cover by forbs, and soil moisture. Nest fields had less grass cover (19.9%) than avoided fields (31.9%). But forbs were greater in nest fields (15.5%) than in the others (3.5%). Rush and sedge cover were not different between field types (10–24% rushes).

Nesting curlews avoided nesting in fields where only 3% of the ground surface was dry but nested in fields that were 45% dry. No difference was observed in mean visual obstruction height of vegetation in these fields. These results provided some insight into reasons for differences in curlew populations at the two study sites. Short vegetation was not common at New Fork. Human activities associated with ranging (fertilizing and dragging) were more common at New Fork than at Horse Creek.

DISCUSSION

Vertical vegetation cover is a measure of visual and foraging obstruction to ground birds such as long-billed curlews. These birds utilize areas with low vegetation profile (Bent 1962, Bicak et al. 1982, Redmond 1986). The decline of long-billed curlews parallels an increase in meadow conversion to taller cultivated fields. Curlews, however, do use cultivated fields, particularly if grazing pressure keeps vegetation low. At the Horse Creek study site, conversion to cultivated hay matched in timing and extent an increase in summer pasturing, which provides extremely short vegetation profiles.

Nest sites were analyzed to determine if curlew land-use practices, which were not apparent from the general description of hay meadows, impacted birds. Four land uses reduced the availability of preferred nest sites: seeding in cultivated fields, land leveling in cultivated fields, irrigation, and dragging. Of these, only irrigation and dragging were different between the two sites. Based on the mean placement of nests in 61% grass and 7% bare ground, cultivated hays would seem to provide good cover for curlew nests. Yet, curlews selected microsites of high-grass density rather than whole fields dense in grass. Evidence for this was threefold: (1) 50% of nests were in higher grass cover than occurred overall in their respective nest fields; (2) nest fields had lower grass cover than avoided fields (at New Fork); and (3) curlews avoided nesting in cultivated fields. Thus, while cultivated hays seemed to have increased the availability of preferred ground cover, adequate grass cover was provided by native fields.

Nesting on hummocks could have provided two advantages: better visibility (of predators), and dry nests. Nest flooding must be detrimental because curlews nested in both drier-than-average microsites and drier-than-average fields. Jenni et al. (1982) also found that curlews nested on the most xeric slopes in their study area.

Some observers have claimed that cattle-grazing is beneficial to long-billed curlews because it maintains low vegetation profiles (Sugden 1933, Timken 1969, Pampush 1980, Bicak et al. 1982). Year-long grazing was not helpful to curlews in Idaho (Redmond and Jenni 1982). In Nebraska, curlews were shown to use summer-grazed fields and avoid winter-grazed pastures (Bicak 1977).

Haying is also a mechanism used to obtain shorter vegetation; however, timing is an important factor. When cultivated fields are fertilized and hayed later in the season, harm to nests may not occur, but the birds probably avoid the fields because of taller grass during the time of nest construction (Bicak 1977).

Many authors have mentioned that curlews use agricultural lands, but only Bicak (1977) studied them on hay meadows. Uncultivated rangelands and pastures support most of the continental long-billed curlew breeding population (Johnsgard 1981, Pampush 1980). Curlews rarely nest in alfalfa, crested wheatgrass (*Agropyron cristatum*), or fallow fields (Renaud 1980, Pampush 1980, Jenni et al. 1982). Intensive cultivation and mechanical irrigation are detrimental to curlews or even preclude curlew use (Wolfe 1931, Yocum 1956, Bent 1962, Renaud 1980, Pampush 1980, Jenni et al. 1982).

Prior studies have rarely investigated water in relation to curlews. McCallum et al. (1977) reported that 41% of curlews observed on Colorado prairies were within 100 m of water. They suggested that curlews select nest sites near water, even though these sites are dry in some years (curlews are very nest-site tenacious; Redmond and Jenni 1982). Limited water sources could then explain the patchy distribution of curlews where short-grass habitat is not limiting (McCallum et al. 1977).

Wet meadows were the limiting habitat for curlews in Nebraska's Sandhills (Bicak 1977). These subirrigated meadows supply the abundant invertebrate prey required by curlew broods. As a result, wet-meadow, brood-rearing territories are more intensively defended than hillside nest territories. Other authors have suggested that moisture is required by curlews or that they readily exploit abundant foods on irrigated lands (Bent 1962, Sugden 1933, Forsythe 1970, Renaud 1980, Pampush 1980, Bicak et al. 1982).

The dominant characteristics of the irrigated lands we studied, aside from graminoid vegetation, were ubiquitous water and large insect populations (predominantly mosquitoes). These insects began emerging on 13 June 1982 at Horse Creek and were extremely numerous by 17 June.

The irrigated hay meadows used by curlews in this study correspond to Pampush's (1980) mixed-grass meadow habitat type. He found curlews on this habitat in the Upper Snake River Basin and other parts of eastern Idaho, as well as Malheur National Wildlife Refuge in Oregon. Cameron (1907) described similar curlew habitat in south central Montana where "tributary creeks . . . rise into pine hills which enclose wide parks." McCallum et al. (1977) documented curlew nesting in the "large, high altitude (over 7,500 ft [2,280 m]) unforested valley" of North Park, Colorado. Subirrigated meadows in North Park are similar to the Upper Green River Basin. Bicak (1977) and Forsythe (1972) also documented curlew use of wet pastures and hay meadows in Nebraska and Utah.

Dragging hay meadows to break up cow manure appeared to be detrimental, as this process in Wyoming occurred at about the time of nesting. Dragging has declined drastically since 1960 at Horse Creek. Prior to 1960, 75 to 85% of all meadows were dragged. Then, as ranch sizes increased (by conglomeration) and hired help decreased, Horse Creek ranchers stopped dragging their fields. Dragging declined to 44% in the 1960s and to only 8% (or four fields) by 1975. Fuel prices, shifts to cultivated hay (not grazed enough to warrant dragging), and summer pasturing have virtually eliminated this 80-year-old practice from Horse Creek. Dragging is essentially unchanged at New Fork (still 85%).

Since few fields are dragged at Horse Creek, manure piles are abundant. Curlews place their nests near manure piles, if they are available; and successful nests are slightly closer than failed nests to manure (though not significantly closer). This tendency to nest near manure has been documented (Silloway 1900, Bent 1962, Wolfe 1931, Sugden 1933, Allen 1980). Nesting near or on conspicuous objects like manure piles camouflages the curlews from aerial predators.

In summary, cultivated fields provided the preferred grass and bare ground but not hummock nest sites. (High vertical cover and fertilization could also limit cultivated-hay nesting, even though grazing and dragging disturbances were absent.) Conscribed irrigation at New Fork provided a greater area of dry soil for nests. Conversely, Horse Creek had more fields with conspicuous manure piles for nest sites and fewer dragging disturbances. As a result of availability of habitat—mixed fields with adequate, but not tall, grass cover and fields with elevated points—curlews seemed to be more successful in nesting and could thereby maintain their populations. Disturbances such as dragging during nesting could destroy nests. Grazing during incubation and field fertilization were correlated with nest failures and a declining population of curlews.

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ESTIMATES OF SITE POTENTIAL FOR PONDEROSA PINE BASED ON SITE INDEX FOR SEVERAL SOUTHWESTERN HABITAT TYPES

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ABSTRACT.—Estimates of site potential for ponderosa pine based on measured site indexes in 416 stands are compared between seven habitat types and one community type. No significant differences in mean site index are found between the habitat types studied. The habitat types are classified into high or moderate site potential classes based on mean site indexes.

Ponderosa pine (*Pinus ponderosa* Laws.) is the most important commercial timber species in the southwestern United States. Ponderosa pine forests occupy the largest area of commercial forest land in Arizona and New Mexico (Choate 1965, Spencer 1966). Ponderosa pine forests reach their maximum development in the Southwest at elevations between 7,000 and 7,800 feet, but also occur at higher and lower elevations (ranging from 6,000 to 8,500 feet) (Schubert 1974). At the lower elevations ponderosa pine forests intergrade into pinyon-juniper forests. At higher elevations, ponderosa pine grades into the Douglas-fir and white fir forest types (Sheppard et al. 1983).

Because of their commercial value, ponderosa pine forests are intensively managed for timber production in the Southwest. Many management decisions are based on site class or quality classifications. Classification of land into site quality or production potential classes provides a useful means for identifying areas where the potential for improved production is greatest (Schubert 1974). In addition, recently developed growth and yield simulation models for southwestern ponderosa pine rely on site quality determination as an important variable for predicting yields over time (Edminster 1978, Larson and Minor 1983).

Site index is currently the most widely used method of evaluating site quality or potential productivity of forest lands in the United States (Jones 1969, Husch et al. 1972, Daubenmire 1976). Site index is based on the average heights of dominant and codominant trees at a specified index age (usually 50 or 100 years). Because stands of the index age are seldom encountered, site index curves are constructed to allow for estimation of site index for stands older or younger than the index age by interpolation between curves. Site index curves describe the height growth of hypothetical trees of specified site indexes.

Because Meyer's (1961) site curves for ponderosa pine tend to underestimate site quality for the species in the Southwest (Schubert 1974), Minor's (1964) ponderosa pine site curves for Arizona and New Mexico are more frequently used for site potential estimates. Minor's curves are developed for dominant trees with breast-height ages of 20 to 140 years and site classes from 40 to 100 feet. Site index classes over 100 can be calculated using an equation presented by Minor (1964).

The use of habitat types (Daubenmire 1952) to classify forest vegetation is gaining acceptance by land managers and researchers in the western United States (Layser 1974, Pfister 1976, Pfister and Arno 1980). One of the primary uses of habitat types is in timber management where they are used to compare regeneration success, succession patterns, cutting methods, and timber productivity and to develop guidelines for collecting seed and plant nursery stock (Pfister and Arno 1980).

The use of habitat types to predict forest site productivity potential or site quality is proposed by several investigators. Differences in the rate of height growth by habitat type are demonstrated for several tree species

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(Daubenmire 1961, Deitschman and Greene 1965, Stanek 1966, Stage 1975, Hoffman 1976, Monserud 1984). Significant differences between site indexes are also shown for habitat types (Stanek 1966, Stage 1975, Hoffman 1976, Mathiasen et al. 1986). Pfister et al. (1971, 1977) and Steele et al. (1981) use site index curves and normal yield tables to estimate yield capability for habitat types in Montana and Idaho.

Habitat type classifications are recognized for southwestern ponderosa pine forests and for forest types where ponderosa pine is often associated with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and white fir (*Abies concolor* [Gord. & Glend.] Lindl.) (Alexander 1985). However, little information is available for ponderosa pine site quality for recognized southwestern habitat types (Moir and Ludwig 1979, Hanks et al. 1983, Fitzhugh et al. 1984, DeVelice et al. 1986). Schubert (1974) provides a summary of the silviculture of southwestern ponderosa pine and emphasizes the need for tying growth and yield simulation models to habitat types. Because site quality is a key variable in ponderosa pine growth and yield models, site quality estimates for different habitat types are needed for the Southwest. This study provides additional quantitative data on site quality based on site index measurements for ponderosa pine for several southwestern forest habitat types and one community type.

TABLE 1. Southwestern ponderosa pine, Douglas-fir, and white fir habitat and community types sampled. Refer to Literature Cited for full reference to footnote citations.

Ponderosa Pine Habitat Types
PIPO/MUVI:*Pinus ponderosa/Muhlenbergia virescens*[5]
PIPO/FEAR:*Pinus ponderosa/Festuca arizonica*[3,4,5]
PIPO/BOGR:*Pinus ponderosa/Bouteloua gracilis*[3,4,5]
PIPO/QUGA:*Pinus ponderosa/Quercus gambelii*[1,3,4,5]

Ponderosa Pine Community Types
PIPO/POLO:*Pinus ponderosa/Poa longiligula*[5]

Douglas-fir Habitat Types
PSME/FEAR:*Pseudotsuga menziesii/Festuca arizonica*[2]

White Fir Habitat Types
ABCO/QUGA:*Abies concolor/Quercus gambelii*[1,3,4]
(*Abies concolor-Pseudotsuga menziesii/Quercus gambelii*[6])
ABCO/BERE:*Abies concolor/Berberis repens*[7]
(*Abies concolor-Pseudotsuga menziesii/* [sparse][6])

[1] Alexander, Ronco, Fitzhugh, and Ludwig 1984.
[2] Alexander, Ronco, White, and Ludwig 1984.
[3] DeVelice et al. 1986.
[4] Fitzhugh et al. 1984.
[5] Hanks et al. 1983.
[6] Moir and Ludwig 1979.
[7] Youngblood and Mauk 1985.

METHODS

Total height and age at breast height were measured for two to six vigorously growing dominant or codominant ponderosa pines in 416 stands representing the southwestern ponderosa pine (314), white fir (92), and Douglas-fir (10) forest types. Trees with visible signs of abiotic, insect, or disease damage were not selected as site trees. The following information was recorded for each stand: national forest, location (township, range, and section), elevation (nearest 100 feet), aspect (four cardinal directions), slope (nearest 5%), slope position (flat, bottom, ridge, slope), and habitat type (HT) (Moir and Ludwig 1979; Hanks et al. 1983; Alexander et al., Lincoln National Forest, 1984; Alexander et al., Douglas-fir habitat, 1984; Alexander et al., Cibola National Forest, 1984; Fitzhugh et al. 1984; Youngblood and Mauk 1985; DeVelice 1986). A total of seven habitat types and one community type (CT) were sampled (Table 1). Stands sampled were located in the Apache (34 stands), Coconino (77 stands), and Kaibab (54 stands) national forests, Arizona; the Carson (36 stands), Cibola (15 stands), Gila (8 stands), Lincoln (11 stands), and Sante Fe (68 stands) national forests, New Mexico; and the San Juan National Forest, Colorado (113 stands).

Site indexes were determined from average total height and breast height age data for each stand using the ponderosa pine site index curves developed by Minor (1964). Site indexes for stands with site indexes greater than 100 feet were calculated using the site index equation presented by Minor (1964). Mean site index and standard deviation were calculated for each habitat type and community type sampled. A one-way analysis of variance, with $p = .05$, was used to compare mean site indexes among habitat types. The Student-Newman-Keuls test was applied to the analysis to determine where significant differences occurred.

RESULTS

Mean site indexes ranged from a low of 74.3 for the PIPO/BOGR HT to a high of 87.0 for

TABLE 2. Mean ponderosa pine site indexes, standard deviations, 95% confidence limits, and site potential classes by habitat and community type.

Habitat type	Number of stands	Mean[1]	95% confidence limits	Site potential class
PSME/FEAR	10	87.0 ± 12.5	78.1 – 95.9	High
PIPO/FEAR	112	83.6 ± 11.2	81.5 – 85.7	High
ABCO/QUGA	72	83.5 ± 11.1	80.9 – 86.1	High
PIPO/QUGA	135	82.3 ± 15.1	79.8 – 84.9	High
PIPO/MUVI	12	81.1 ± 8.6	75.6 – 86.6	High
ABCO/BERE	20	79.3 ± 12.7	73.3 – 85.3	High
PIPO/POLO	16	79.7 ± 8.5	75.2 – 84.2	High
(Comm. Type)				
PIPO/BOGR	39	74.3 ± 13.4	69.9 – 78.6	Moderate
TOTAL	416			

[1] No significant differences were detected between mean site indexes using the Student-Newman-Kuels test, p = .05.

the PSME/FEAR HT (Table 2). Standard deviations ranged from 8.5 for the PIPO/POLO CT to 15.1 for the PIPO/QUGA HT. None of the mean site indexes was found to be significantly different at the p = .05 level. Ponderosa pine forests in Arizona and New Mexico are grouped into three site classes for management reasons by the U.S. Forest Service (Southwest Region). The groupings are based on potential cubic feet/acre/year productivity estimates and use Minor's (1964) site index curves: Site Class 1 represents site indexes above 75, Site Class 2 represents site indexes from 55 to 74, and Site Class 3 represents site indexes less than 55. Although the mean site indexes for the habitat type sampled in this study were not significantly different, site potential classes for ponderosa pine were assigned for the habitat types based on mean site indexes and the above site class system used by the Forest Service. Our high and moderate site potential classes correspond to Site Class 1 and Site Class 2, respectively (Table 2).

DISCUSSION

Site index is currently the most widely accepted method of evaluating site quality in the United States. Several investigators report significant differences in site index between habitat types for several tree species (Stanek 1966, Roe 1967, Hoffman 1976, Mathiasen et al. 1986). However, our results indicate no significant differences between mean site indexes for ponderosa pine between the seven habitat types and one community type sampled in this study. Daubenmire (1961) rejects the use of ponderosa pine site index curves for predicting potential productivity of habitat types because he found large variations between the site indexes of contiguous young and old stands of ponderosa pine in burned areas representing homogeneous habitats. Daubenmire reports that ponderosa pine grows faster than site index curves predict. Other investigators report similar findings for other tree species (Ilvessalo 1927, 1937, Carmean 1956). In addition, stand density, soil variation, and early suppression of trees can affect the validity of site quality determinations based on site index curves (Jones 1969). Therefore, our estimates of site quality for ponderosa pine presented here and for Douglas-fir (Mathiasen et al. 1986) based on site index may be underestimating actual site potential for the habitat types we have sampled thus far. However, site index is considered to be the best practical indicator of relative site quality at this time (Hodgkins 1956, Vincent 1961, Jones 1969, Husch et al. 1972).

Based on the U.S. Forest Service site class system and our mean site indexes for ponderosa pine, all but one of the habitat types sampled in this study are classified as high site potential (Class 1) habitat types. Although there was a large degree of variation in site index for each of the habitat types sampled (standard deviations averaged 11.6), site potential ranges are represented best by their 95% confidence limits; most of the habitat types' 95% confidence limits are within the high site potential class (Table 2).

In their descriptions of habitat type classifications, several investigators report site quality estimates for ponderosa pine in southwestern forest habitat types (Moir and Ludwig 1979, Hanks et al. 1983, Alexander et al. 1984, Fitzhugh et al. 1984, Youngblood and Mauk 1985, DeVelice et al. 1986). Our estimates of site quality for ponderosa pine by habitat type support the estimates made by Fitzhugh et al. (1984) and Hanks et al. (1983) for the PIPO/FEAR HT (moderate to high). However, DeVelice et al. (1986) report low site potential for ponderosa pine in the PIPO/FEAR HT in northern New Mexico and southern Colorado. Fitzhugh et al. (1984) report high potential for ponderosa pine in the PIPO/MUVI HT. Our results essentially agree with their estimate. Moir and Ludwig (1979) report stands with what they consider low site potential for ponderosa pine (site index of about 65) in the ABCO/QUGA HT. DeVelice et al. (1986) and Hanks et al. (1983) report low or poor site potential for the ABCO/QUGA HT. However, our site index data for this habitat type indicate high site potential for ponderosa pine. Our findings also indicate higher site potential for ponderosa pine in the PSME/FEAR HT (high site potential) than reported by DeVelice et al. (1986) (low site potential). Hanks et al. (1983) report that the PIPO/BOGR HT probably represents the lowest site potential of any ponderosa pine habitat type in the Southwest. However, our results indicate that site potential is moderate for this habitat type. Site potential estimates for ponderosa pine have not been reported for one of the habitat types and the community type sampled in this study. Based on our site index data, site quality for the ABCO/BERE HT and the PIPO/POLO CT is high. Hanks et al. (1983) state that the PIPO/POLO CT is "suitable" for timber production, and we agree with their evaluation.

The reasons for differences in ponderosa pine site quality estimates for southwestern forest habitat types by various investigators are primarily the result of geographic variation in site indexes (Monserud 1985) or differences in criteria for interpreting site index data in relation to site quality. Hanks et al. (1983) and Fitzhugh et al. (1984) do not explain the basis for their estimates of ponderosa pine site quality, but their estimates do not appear to be based on quantitative site index data collected during their field work. DeVelice et al. (1986) base their estimates on site index data and rate ponderosa pine site quality using the standard U.S. Forest Service Southwest Region site class groupings described earlier. We also base our site potential estimates for ponderosa pine on the Forest Service site class groupings and suggest that future habitat type classifications adopt this system to have consistent criteria for estimating site quality for habitat types in the Southwest. Even though we used the same site class system, our estimates of ponderosa pine site potential vary a great deal from those of DeVelice et al. (1986). The most probable explanation for the differences between our site potential estimates and those of DeVelice et al. is that ponderosa pine and Douglas-fir tend to demonstrate much lower site indexes in the Sangre de Cristo Mountains of northern New Mexico and southern Colorado (Moir and Ludwig 1979), where DeVelice et al. (1986) collected much of their site index data. Therefore, site quality estimates for southwestern habitat types based on habitat type classification studies from specific geographic areas or national forests may not adequately represent the range in site potential classes encountered in the Southwest.

Several authors discuss the problems with using site index data to estimate site quality (Hodgkin 1956, Vincent 1961, Daubenmire 1961, 1976, Jones 1969). Although site index data are generally regarded as a somewhat rough estimate for productivity potential of forest land, they are still accepted as the most practical and direct method for evaluating relative productivity (Vincent 1961, Jones 1969, Husch et al. 1972, Daubenmire 1976). Site quality estimates for forest habitat types based on site index data are still applicable to current forest management procedures, but because large variations occur in site indexes within habitat types, the use of habitat types for predicting timber productivity potential is imprecise. However, because timber productivity is primarily estimated from site index information, site class estimates based on site index data should be determined for additional southwestern habitat types and other commercially important tree species. In addition, our site quality estimates for ponderosa pine and for Douglas-fir (Mathiasen et al. 1986) for several southwestern forest habitat types should be supported or modified if necessary with additional site index data collected from stands classified by habitat type.

The development of separate site index curves for different habitat types may improve the accuracy of site index as an estimate of site quality (Monserud 1984). Furthermore, the development and subsequent validation of growth and yield simulation models using growth coefficients based on habitat types (Stage 1973, 1975) may improve productivity estimates for habitat types.

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SOIL NEMATODES OF NORTHERN ROCKY MOUNTAIN ECOSYSTEMS: GENERA AND BIOMASSES

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ABSTRACT.—Soil nematode populations were larger and more diverse in two grasslands than in three forests of the northern Rocky Mountains. As we moved from *Festuca idahoensis* grassland through progressively higher zones of vegetation dominated by *Artemisia tridentata*, *Populus tremuloides*, and *Pseudotsuga menziesii*, and then to *Abies lasiocarpa* forests, numbers of nematode genera declined from 31 to 26 to 20 to 21 to 13; numbers of individuals in the top 50 cm of the soil were 6.0, 5.3, 1.7, 1.5, and 1.6 million/m^2, and biomasses of nematodes in the top 50 cm of the soil were 0.83, 0.88, 0.58, 0.35, and 0.19 g/m^2. Biomasses of nematodes were often well correlated with root biomass as well as soil depth; of the nematodes in the 0–50-cm horizon, 38 to 70% were in the 0–20-cm layer. The effects of light grazing on nematode populations were small or nonexistent.

While the plant component of major Rocky Mountain communities has been characterized (Mueggler and Stewart 1979, Pfister et al. 1977), their soil nematode composition has not been described (cf. Table 1). To repair this deficiency, we have compared the generic composition, densities (number/m^2) by feeding group, and biomasses (g/m^2) by feeding group of nematodes in major vegetation types spanning the altitudinal zone from foothills to timberline. On a complex gradient of increasing altitude, increasing precipitation, and decreasing temperature (Weaver 1980), these include: *Festuca idahoensis* grasslands, *Artemisia tridentata* shrublands, *Populus tremuloides* forests, *Pseudotsuga menziesii* forests, and *Abies lasiocarpa* forests. Strengths of our study include the diversity of ecosystems compared, the use of uniform methods to compare them, and the sampling of a thicker soil layer (0–50 cm) than is usually studied (cf. Table 1).

METHODS

To describe soil nematode populations associated with Rocky Mountain vegetation, we sampled soils under near-climax communities representing major vegetation zones along the altitudinal gradient. From foothills upward, these were *Festuca idahoensis–Agropyron caninum*, *Artemisia tridentata–Festuca idahoensis*, *Populus tremuloides–Poa pratensis*, *Pseudotsuga menziesii–Symphoricarpos alba*, and *Abies lasiocarpa–Vaccinium scoparium* habitat types. All stands were in the Bridger Mountains, within 22 km of Bozeman, Montana, and at altitudes of 2,330, 1,570, 1,810, 1,650, and 1,820 m, respectively. Pfister et al. (1977) and Mueggler and Stewart (1979) describe the plant associations indicated. Soil water regimes of all stands (Weaver 1977) and nutrient regimes of the *Artemisia*, *Pseudotsuga*, and *Abies* stands (Weaver and Forcella 1979) have been characterized previously. The soils were classified as Typic Cryoborolls, Pachic Argiborolls, Udic Haploborolls, Typic Haploborolls, and Mollic Cryoboralfs, respectively.

Soil cores used in characterizing the nematode populations were collected in all stands on 30 July 1973. A second sample was collected at the Festuca-Agropyron site on 2 October 1972. At each site six cores were taken using a soil-sampling tube with a 2.1-cm inside diameter. Cores were taken to a depth of 50 cm at 3-m intervals along a line passing through the stand studied. Each core was divided into 10-cm increments: 0–10 cm, 10–20 cm, etc. The cores were refrigerated at 4 C until they were analyzed.

Nematodes were extracted from the soil by wet screening followed by Baermann funnel extraction (Christie and Perry 1951). The efficiency of the wet screening was determined

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TABLE 1. Nematode numbers and biomasses in various vegetation types.

Vegetation type		Densities (millions/m^2)	Biomasses (g/m^2)	Depth[1] (cm)	Source
Desert	Mojave	0.4–1.1	0.1–0.2	30	Freckman et al. 1975
	Colorado	0.5–0.8	0.1	30	Freckman et al. 1975
Grasslands	Andropogon	0.1–0.3	0.2–1.5	20	Coleman 1971
		0.1–0.5	0.5–3.0	80	Coleman 1971
	Phalaris	0.1–0.3	—	25	King and Hutchinson 1976
	Swiss	—	5.0	15	in Banage 1963
	Danish	4–20	6–18	5	in Banage 1963
	Irrigated field	0.8–1.7	0.15	20	Freckman et al. 1975
	Artemisia-Agropyron	4.7–5.3	0.4–0.5	40	Smolik and Rodgers 1976
	Agropyron-Büchloe	3.8–7.9	0.5–1.8	60	Smolik 1974
Deciduous forests					
	Beech	0.4	0.08	6	Phillipson 1977
	Beech	1.1	0.28	6	Yeats 1972
	Beech	12	4.0	25	in Banage 1963
	Oak	30	15	25	in Banage 1963
	Oak-hornbeam	—	4–13	?	Saly 1975
	Liriodendron	1–6	0.6–1.4	16	McBrayer et al. 1977
Coniferous forests					
	Picea	0.01	—	?	Eroshenko 1976
	Pseudotsuga	1.3	—	16	McBrayer et al. 1977
Moor	Danish	1–3	1.5–4.5	5	in Banage 1963
	British	2–3	0.5–0.8	6	Banage 1963
Tundra	Bare soil	0.07	0.3	85	Kuzmin 1976
	Bare soil	0.01	—	10–100	Chernov et al. 1977
	Moss lichen	2–4	—	10–100	Chernov et al. 1977
	Moss	0.5	—	6	Spaull 1973
	Moss	0.6–3	6–31	85	Kuzmin 1976
	Herb-grass	0.8–8	1.1–7.5	85	Kuzmin 1976
	Deschampsia	7.4	—	6	Spaull 1973

[1] Sampling was from the top of the soil to the depth given.

by reextracting the soil sample. Efficiency of the Baermann funnel was established by examining approximately 10% of the residues to determine the number of nematodes that failed to pass through the screen. Nematode numbers were then corrected for the overall extraction efficiency, which varied with vegetation type from 60 to 70%. Density estimates were made by counting the number of nematodes (60X magnification) in three 1-ml aliquots of a 50-ml suspension on Scott hookworm larvae counting slides. Biomass estimates were made following the method of Andrassay (1956) and were converted to dry weight by multiplying by 0.25 (Smolik 1974). Generic identifications and measurements for biomass determinations were obtained from permanent mounts (Thorne 1961) of approximately one thousand randomly selected individuals. Nematodes were assigned to feeding groups by reference to standard catalogues listed by Smolik (1974).

Although our study is based on samples taken on one date near midsummer (30 July 1973), we believe the data fairly approximate the general numbers, biomasses, and generic compositions that might be found in another summer month or in the same month of another year. The following statements support our belief. (1) Most studies in which successive samples have been taken from sites with undisturbed vegetation show relatively small differences (less than a factor of two) between nematode populations in successive summer months: differences observed by Coleman (1971), King and Hutchinson (1976), Phillipson et al. (1977), Banage (1963), and Ferris and McKenry (1976) were not statistically significant; some differences observed by Yeats (1972) were statistically significant; differ-

TABLE 2. Nematode genera present in five vegetation types.

Feeding group and genus	Community type					
	FEID[1]	FEID[2]	ARTR[1]	POTR[1]	PSME[1]	ABLA[1]
Herbivore						
Ditylenchus	+	+	+	+	+	+
Helicotylenchus	+	+	+	+	+	+
Merlinius	+	+	+	+	+	+
Tylenchus	+	+	+	+	+	+
Tylenchorhychus	+	+	+	+	+	
Aglenchus	+	+	+	+		
Nothotylenchus	+	+	+	+		
Dorylaimellus	+	+	+			
Paratylenchus	+	+	+			
Tylencholaimellus	+	+	+			
Criconemoides	+	+				
Enchodelus	+	+				
Hemicycliophora	+	+				
Pratylenchoides	+					
Axonchium		+				
Diphtherophora			+	+		
Xiphinema			+	+		
Trichodorus				+	+	
Tylencholaimus	+				+	
Boleodorus		+	+		+	
Leptonchus					+	
Number of genera	15	15	13	11	9	4
Predaceous						
Aporcelaimellus	+	+	+	+	+	+
Eudorylaimus		+	+	+	+	+
Dorylaimoides	+		+	+	+	
Nygolaimus	+	+	+			
Thonus	+	+				
Mesodorylaimus		+				
Tripyla					+	
Mylonchulus				+		+
Miconchus						+
Mononchus	+	+				+
Number of genera	5	6	4	4	4	5
Microvore						
Acrobeloides	+	+	+	+	+	+
Plectus	+	+	+	+	+	+
Aphelenchoides	+	+	+		+	+
Panagrolaimus		+	+	+		+
Aphelenchus	+	+	+	+		
Eucephalobus	+	+	+	+		
Acrobeles	+	+	+			
Bastiani		+				
Prismatolaimus		+				
Wilsonema	+					
Anaplectus	+	+			+	
Chiloplacus	+	+			+	
Rhabditis		+			+	
Cervidellus	+		+		+	
Cephalobus	+	+	+		+	
Number of genera	11	13	9	5	8	4
Total genera	31	34	26	20	21	13

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[1] Ungrazed vegetation types were *Festuca idahoensis* (FEID), *Artemisia tridentata* (ARTR), *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), and *Abies lasiocarpa* (ABLA).

[2] Grazed vegetation of an adjacent *Festuca idahoensis* stand (FEID).

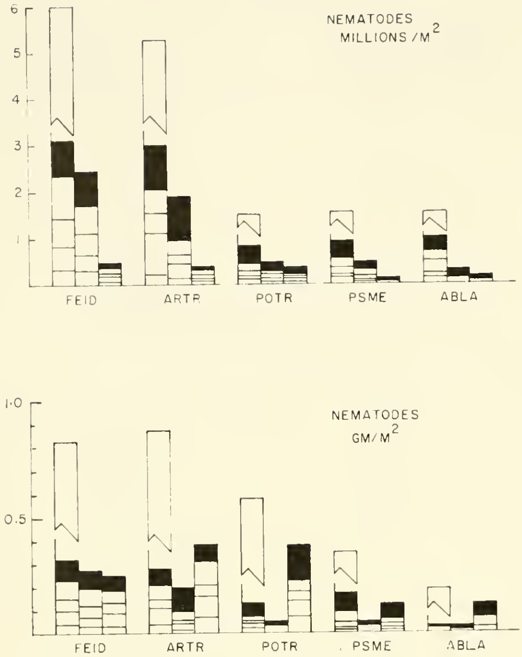

Fig. 1. Nematode numbers and biomasses in five vegetation types: A, Nematode numbers in millions; B, Nematode biomasses in grams per square meter. The first bar in each type presents herbivore data, the second microvore data, and the third predator data. Each bar is subdivided into a shaded portion and four clear portions below it indicating successively lower 10-cm horizons. Above the first bar is an unshaded bar indicating total nematode numbers or biomasses. The vegetation types are *Festuca idahoensis* (FEID), *Artemisia tridentata* (ARTA), *Populus tremuloides* (POTR), *Pseudotsuga menziesii* (PSME), and *Abies lasiocarpa* (ABLA).

ences observed by Smolik and Rodgers (1976) and McBrayer (1977) might have been statistically significant if they had been tested. (2) Numbers and biomasses measured in our *Festuca idahoensis* grassland changed little with season; on 2 October 1972, for example, they were 1.2 times as large as those measured on 30 July 1973. (3) Weather data from a station representative of the region (USDC 1973, Bozeman MSU, Montana) were normal: April–July precipitation was 100% of normal, June precipitation was 140% of normal, and July precipitation was 33% of normal; the average May temperature was normal, the average June temperature was 1.2 C above normal, and the average July temperature was 0.8 C above normal.

Root biomass data correlated with nematode population parameters were measured by coring, washing out small roots (< 1 mm), and determining their ash-free weights. Detailed methods and results were reported by Weaver (1977).

RESULTS AND DISCUSSION

DIVERSITY.—The generic diversity of plant-feeding and microbe-feeding nematodes declined as we moved from steppelands (*Festuca* and *Artemisia*) to a *Populus* forest to coniferous forests (*Pseudotsuga* and *Abies*), but the diversity of predaceous nematodes remained constant (Table 2). The difference appears to be due principally to the failure of steppe genera under forest conditions, since the number of genera endemic to steppelands (15) was three times greater than the number restricted to forest lands (5). The major nematode genera appearing in each vegetation type are listed in Table 2.

DENSITY.—Total numbers of nematodes present in the upper 50 cm of the soil declined from grasslands to forests (Fig. 1); they were 6.0, 5.3, 1.7, 1.5, and 1.6 million/m^2 in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* stands, respectively. The nematodes were similarly partitioned into plant-feeders, microbe-feeders, and predators in steppe vegetation (55, 38, and 7%, respectively) and coniferous forests (65, 25, and 10%, respectively). Given differences in the methods used and the depths considered, our data generally agree with those from other regions (Table 1). Note especially that Egunjobi (1971) and Razzhivin (1976) also found lower nematode densities in forests than in grasslands and that Novikova (1970) also observed similar nematode densities in deciduous and coniferous forests.

BIOMASS.—Total nematode biomasses present in the upper 50 cm of the soil declined from grasslands to forests (Fig. 1, Table 3); they were 0.83, 0.88, 0.58, 0.35, and 0.19 g/m^2 in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* vegetation, respectively. These biomasses are similar to those reported in other regions (Table 1). The nematodes were similarly distributed among plant-feeders, microbe-feeders, and predators in steppe communities (35, 28, and 37%, respectively) and coniferous forests (35, 15, and 50%, respectively). These masses may be better appreciated by comparing them with the

TABLE 3. Mean[1] nematode and root biomasses (g/m^2) of five vegetation types.[2]

		Soil depth (cm)						CV^3	r^{2,4}
		0–10	10–20	20–30	30–40	40–50	0–50		
FEID	herbivore	0.087	0.079	0.056	0.065	0.035	0.322	0.10	0.59
	microvore	0.080	0.066	0.049	0.040	0.029	0.266	0.13	0.83**
	predator	0.056	0.056	0.042	0.061	0.033	0.247	0.05	0.14
	total	0.223	0.201	0.147	0.166	0.097	0.835	0.06	0.62**
	root	902.0	391.0	143.0	51.0	95.0	158.2	0.01	
ARTR	herbivore	0.056	0.061	0.044	0.075	0.047	0.283	0.12	0.01
	microvore	0.102	0.033	0.019	0.035	0.014	0.203	0.16	0.87**
	predator	0.070	0.102	0.059	0.093	0.075	0.399	0.14	0.00
	total	0.228	0.196	0.122	0.203	0.136	0.885	0.03	0.55*
	root	202.0	118.0	58.0	54.0	44.0	476.0	0.03	
POTR	herbivore	0.060	0.021	0.012	0.021	0.021	0.135	0.35	0.90**
	microvore	0.022	0.004	0.010	0.010	0.006	0.052	0.22	0.68**
	predator	0.017	0.040	0.038	0.065	0.079	0.239	0.22	0.56*
	total	0.099	0.064	0.060	0.096	0.106	0.426	0.19	0.24
	root	355	409	37	12	23	836	0.23	
PSME	herbivore	0.083	0.037	0.033	0.007	0.009	0.169	0.19	0.96**
	microvore	0.021	0.014	0.008	0.007	0.003	0.053	0.21	0.80**
	predator	0.064	0.026	0.028	0.007	0.005	0.130	0.17	0.96**
	total	0.168	0.077	0.069	0.021	0.017	0.352	0.13	0.95**
	root	231	81	88	42	48	490	0.14	
ABLA	herbivore	0.010	0.005	0.008	0.003	0.004	0.030	0.48	0.67**
	microvore	0.021	0.006	0.001	0.004	—	0.032	0.36	0.90**
	predator	0.064	0.041	0.020	—	—	0.125	0.42	0.95**
	total	0.095	0.052	0.029	—	—	0.176	0.35	0.99**
	root	245	123	75	45	57	545	0.06	

[1] Average coefficients of variation for herbivore-microvore-predator and root data are FEID (19–1%), ARTR (28–40%), POTR (55–33%), PSME (41–45%), and ABLA (76–40%).

[2] Vegetation types are FEID = *Festuca idahoensis*, ARTR = *Artemisia tridentata*, POTR = *Populus tremuloides*, PSME = *Pseudotsuga menziesii*, and ABLA = *Abies lasiocarpa*.

[3] Coefficients of variation (SD/X) for the 0–50 cm layer.

[4] The square of the correlation coefficient (r^2) of nematode biomass against root biomass by layer. Statistical significance is indicated by asterisks. ** = significant at the 1% level, and * = significant at the 5% level.

biomass of cattle grazing in a *Festuca* meadow, that is, approximately 4–5 g/m^2 on an annual basis.

COMMUNITY STRUCTURE.—The functional composition—microvore, phytovore, predator—of the nematode population showed no consistent changes with changes in community type. Phytovores comprised about 60% of the herbivore (microvore and phytovore) biomass; this proportion was 56, 58, 67, 78, and 50% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* communities, respectively. Predator weights usually exceeded 50% of the herbivore weights; they were 42, 82, 216, 60, and 197% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies* communities, respectively. The large predator/herbivore ratios suggest that herbivores turn over rapidly, that the predators consume other foodstuffs including plant material (Smolik 1974), and/or that the predators have low respiration rates (Klekowski et al. 1972). The pyramid (predator/herbivore ratio) of biomass is less steep than the number pyramid because predators (0.96 g/million) are nine times larger than herbivores (0.11 g/million). For comparison, the weight of a predatory wolf is about 40 kg, and his herbivorous prey range in weight from 0.03 kg (voles) to 5 kg (rabbits) to 100 kg (deer) to 700 kg (bison) (Burt and Grossenheider 1964).

ENVIRONMENTAL FACTORS CORRELATED WITH NEMATODE DISTRIBUTION.—We do not know what environmental factors are responsible for the decline in nematode diversity, numbers, and biomass from grasslands to forests. Evidence suggesting that low temperatures may be the controlling factor is summarized below. (1) Soil temperatures, like nematode numbers, are lower under our forests than in adjacent (or lower) grasslands (Munn et al. 1979). (2) Our data (Fig. 1, Table 3) are inconsistent with other obvious hypotheses. Soil water, said to favor nematodes (McBrayer et al. 1977), becomes more available as one moves from nematode-rich steppelands to nematode-poor forests (Weaver 1977). Soil organic matter and pH are lower in nematode-poor coniferous forests, but not in nematode-poor aspen forests, than in nematode-rich steppelands. Though they are high in nematode-rich *Festuca* grasslands, root biomasses of the nematode-rich *Artemisia* community did not exceed those of the nematode-poor forests. Nutrient elements (e.g., N, P, K) are probably available in larger quantities in nematode-rich steppelands, and in nematode-poor aspen forests, than in nematode-poor coniferous forests (Weaver 1979). (3) Egunjobi's (1971) observation that nematodes were fewer in forests of New Zealand than in adjacent cleared land planted to grasses supports the temperature hypothesis: soils of the cleared area probably differ little in pH, organic matter content, nutrient availabilities, water availabilities, etc., but they are probably warmer. (4) An alternate, but doubtful, hypothesis is that trees have evolved nematode-inhibiting structures or chemicals, perhaps in response to a greater initial susceptibility associated with their relatively long lives.

Total nematode biomasses decreased regularly with depth in *Festuca*, *Pseudotsuga*, and *Abies* communities, but not under *Artemisia* and *Populus* (Table 3). Of nematode biomasses in the 0–50-cm horizon, the 0–20-cm horizon contained 51, 48, 38, 70, and 67% in *Festuca*, *Artemisia*, *Populus*, *Pseudotsuga*, and *Abies*, respectively. Similar decreases were observed by Coleman (1971), who emphasized the need for examination of subsurface horizons, as well as by Smolik (1974) and Ferris and McKenry (1976).

One might expect nematode biomasses to be well correlated with root biomasses, which also decline with depth, either because roots serve as a food source or because warm, moist, oxygen-rich conditions favoring roots should favor nematodes as well. The correlation between microvores and root biomass data from the same sites (Weaver 1977) is highly significant in every vegetation type (Table 3). The correlation of both herbivore and predator biomasses with root biomass was significant in forest communities, but not in steppe communities (Table 3).

Small differences in nematode numbers between grazed and ungrazed parts of our meadow, if they are biologically significant, could be due to light grazing or to the relatively shallow soils of the grazed plots. Total numbers were significantly less at the 1% level in October 1972 (grazed 6.3 million/m^2, ungrazed 7.2 million/m^2) and in July 1973 (grazed 4.8 million/m^2, ungrazed 6.0 million/m^2). Total autumn 1972 biomasses were 1.04 g/m^2 in the grazed area plots and 1.05 g/m^2 in ungrazed plots; total summer 1973 biomasses were 0.72 g/m^2 grazed and 0.83 g/m^2 ungrazed. Numbers of plant-feeders were lower in the grazed plot in both years and significantly so in 1972. Numbers of microbe-feeders were significantly greater in the grazed area in 1973, but were lower in 1972. Numbers of predators were lower in the ungrazed area in 1972, higher in the ungrazed area in 1973, and did not differ significantly between treatments in either year. Plant-feeding nematode biomasses were apparently reduced by grazing in a South Dakota *Agropyron smithii–Büchloe dactyloides* grassland (Smolik 1974), but not in a Washington *Artemisia tridentata–Agropyron spicatum* grassland (Smolik and Rodgers 1976).

CONCLUSIONS

Soil nematode populations were more dense, heavier, and more diverse under steppe than forest vegetation. The decline occurred under both deciduous and coniferous vegetation. The drop in soil temperature may be a major influent. Grazing is apparently not.

Within a soil, nematodes are most numerous in surface horizons. This could be due to conditions which favor roots, to the presence of roots, or to the presence of organisms associated with the roots.

ACKNOWLEDGMENTS

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EVIDENCE FOR VARIABILITY IN SPAWNING BEHAVIOR OF INTERIOR CUTTHROAT TROUT IN RESPONSE TO ENVIRONMENTAL UNCERTAINTY

Rodger L. Nelson[1], William S. Platts[1], and Osborne Casey[2]

ABSTRACT.—The fluctuating characteristics (numbers, biomass, condition, and young-adult ratios) of the Lahontan (Humboldt) cutthroat trout population in Chimney Creek, Nevada, are discussed in relationship to the unpredictable and unstable habitat in which the population occurs. One possible means of adapting to environmental capriciousness, staggered spawning, occurred during 1982, and clues as to the cause of this unusual event are sought by examining the runoff hydrographs of a nearby watershed for 1981 through 1984. The management values of the environmental tolerance of these native trout with respect to restoring viable trout fisheries in degraded Great Basin streams are also considered.

It can be reasonably assumed that organisms are adapted to the habitats in which they occur naturally. Consequently, persistence through time in a natural, yet apparently hostile, environment provides empirical evidence that a species has developed a successful adaptive strategy with respect to prevailing conditions. Mechanisms underlying such adaptation, however, are poorly understood, and conventional thinking may be misleading. For example, if we expect adaptation to occur through specialization, we may find it difficult to explain an organism's adaptation to an environment characterized by unpredictable events. In such situations, in fact, the more profitable adaptive strategy may be maintenance of a high degree of environmental tolerance, such as greater niche breadth (Valentine 1969). It may, therefore, be advantageous for a population to maintain considerable genetic flexibility (Thoday 1959). Genetic flexibility will serve to ensure persistence during periods of marginal habitat conditions and will confer the ability to rapidly exploit unusually favorable conditions; such a population will be resilient but potentially highly unstable (Holling 1973). Such genetic flexibility may be manifested behaviorally and may include reproductive behavior (Wellington 1964). Accordingly, we might expect some apparently unusual population behavior in response to unusually capricious environmental events.

The interior basins of the western United States offer worthy environments in which to study adaptations of native riverine fishes to apparently hostile situations. Climatic conditions are highly unstable over time, and stream flow patterns, though manifesting some seasonal regularity, are often unpredictable in timing, duration, and magnitude. Recent studies of Great Basin streams have revealed exceptional precipitation and consequent runoff events during the past several years (Platts, Gebhardt et al. 1985). Of particular interest in this regard are the cutthroat trout (*Salmo clarki* ssp.) native to the upper Humboldt River Basin in northeastern Nevada. Taxonomically, these trout are generally accorded identity with the Lahontan cutthroat (*S. c. henshawi*), native to the western portion of the Lahontan Basin, comprising the Truckee, Walker, and Carson River drainages of northwestern Nevada and eastern California. Recent work, however, has suggested that it would be more appropriate to assign the populations endemic to the upper Humboldt River system separate subspecific status (Behnke 1979, Platts and Nelson 1983). In this report, we have adopted Behnke's (1979) tentative classification of these fish as Humboldt cutthroat trout.

Habitat requirements of the riverine cutthroat trout in the upper Humboldt drainage are nearly as uncertain as taxonomic designation. Coffin (1982), echoing the words of

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Raleigh and Duff (1981), indicates that optimal riverine cutthroat trout habitat is

> characterized by clear, cold water; a silt-free rocky substrate in riffle-run areas; an approximately 1:1 pool-riffle ratio with areas of slow, deep water; well vegetated stream banks; abundant instream cover; and relatively stable water flow, temperature regimes, and stream banks.

While we have no quarrel with the general applicability of such a statement, it seems too simplistic for conditions characterizing Great Basin streams; riverine populations in the upper Humboldt River Basin persist and even thrive in the absence of any of these criteria (Behnke 1979, Platts and Nelson 1983).

Cutthroat trout are typically regarded as small-stream spawners (Platts 1960, Van Deventer and Platts in press), and both lacustrine and riverine fish may ascend small streams to spawn. Whether this leads to interbreeding between migratory and resident populations is unclear but can probably be assumed. The spring spawning habit allows utilization of small, intermittent streams during high flow periods rather than during undependable late summer and fall when adequate flows are less predictable. Timing of upstream migration may therefore be triggered by peak flows to optimize the resource. Because flooding may be detrimental to egg survival (Seegrist and Gard 1972) and invertebrate food production (Elwood and Waters 1969), however, spawning must ideally occur late enough in the runoff period to minimize the possibility of an unexpected late-season flood. Correspondence between peak flows and upstream spawning migration has been reported for rainbow trout (*Salmo gairdneri* Richardson) in Sagehen Creek, California, by Erman and Hawthorne (1976), and Coffin (1982) stated that Lahontan cutthroat trout ascend streams as flows and water temperatures rise in the spring. Sigler et al. (1983) showed that peak spawning migration of Lahontan cutthroat trout from Pyramid Lake, Nevada, occurred between April and May but over a range of February to July. Lea (1968) reported spawning runs of Lahontan cutthroat trout leaving Independence Lake, California, beginning as early as mid-June and continuing as late as August during years with high stream flow conditions. Another very closely related interior subspecies, the Bonneville cutthroat (*S. c. utah*), has been reported to spawn from late May to mid- to late June, with spawning beginning in the lowest stream reaches and progressing upstream (May et al. 1977).

This paper describes the characteristics of the population of Humboldt cutthroat trout in Chimney Creek, Nevada, during four years of "abnormal" spring flows. We propose this behavior as evidence suggesting plasticity in reproductive behavior as an adaptation to a hostile and capricious environment. Several mechanisms for this adaptive behavior are discussed, and suggestions for future study are proffered.

STUDY AREA

Chimney Creek is a small, occasionally intermittent tributary of Mary's River in northeastern Nevada. Situated approximately 1,950 m above sea level, Chimney Creek serves as a nursery stream for migratory cutthroat trout in Mary's River and also supports a small resident population; no other fish species are present (Platts, Torquemada et al. 1985). Taxonomic studies of the resident fish have not been conducted, but individuals from Mary's River have been reported as pure Humboldt strain, as have individuals from nearby "T" Creek (Coffin 1982).

Climatic conditions around Chimney Creek are typical of the northern Great Basin, with cold, snowy winters and hot, dry summers. Spring snowmelt during the past several seasons has resulted in dramatic alterations to the stream channel (Platts, Gebhardt et al. 1985, Platts, Torquemada et al. 1985). Coffin (1982) reported water temperatures as high as 17 C, and Platts, Torquemada et al. (1985) reported temperatures as high as 13 C as late as mid-October and diurnal fluctuation as high as 8 C. Our data[3] show that water temperatures fluctuate drastically, even in winter, and can be as low as 0.4 C (Fig. 1).

METHODS

Cutthroat trout population sizes in a 548-m section of Chimney Creek were determined

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[3] Collected with Ryan Model J Thermographs. Data on file USDA Forest Service, Intermountain Research Station, Forestry Sciences Lab, Boise, Idaho. The use of trade or firm names in this paper is for reader information and does not imply endorsement by the U S Department of Agriculture of any product or service.

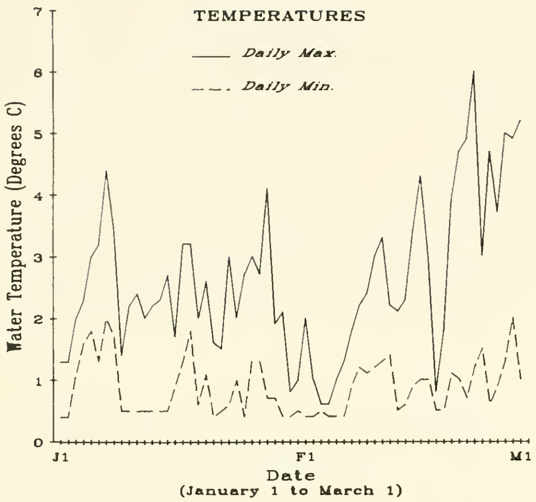

Fig. 1. Midwinter water temperature fluctuations, Chimney Creek, Nevada, 1 January–1 March 1983.

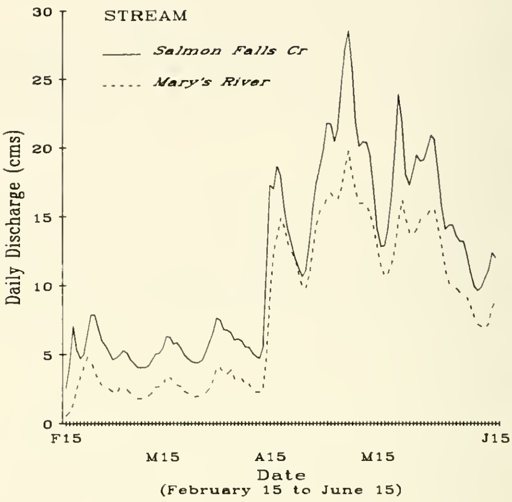

Fig. 2. Stream flow hydrographs from 1982 for Salmon Falls Creek and Mary's River, Nevada.

annually from 1981 through 1984 during mid-August when flows were at their stable, midsummer base level. Smith-Root Model SR-VII battery-powered, direct-current electrofishers were used to collect fish using the four-pass method of Platts et al. (1983). True population sizes were estimated using the maximum-likelihood depletion model (Platts et al. 1983, Van Deventer and Platts 1984). Trout were measured to the nearest millimeter, weighed to the nearest 0.1 g, and returned to the stream.

All fish smaller than 75 mm were considered to be young of the year (YOY) because they formed distinct size-class peaks on length-frequency plots (Bagenal and Tesch 1978); all others were classified as adults. Biomass was determined volumetrically and areally as the product of population estimates and their weight per cubic meter and per square meter of stream, respectively (Platts and Nelson 1983). Volumetric and areal densities were similarly calculated as number per cubic meter and per square meter, respectively. We used volumetric estimates because we feel they more fully represent the three-dimensional character of the stream environment than do conventional estimates based on surface area alone; however, areal estimates have been included for reference. We determined average stream width and depth as described in Platts et al. (1983) to provide additional information about instream water levels as well as to provide density and biomass parameters. Volume was determined

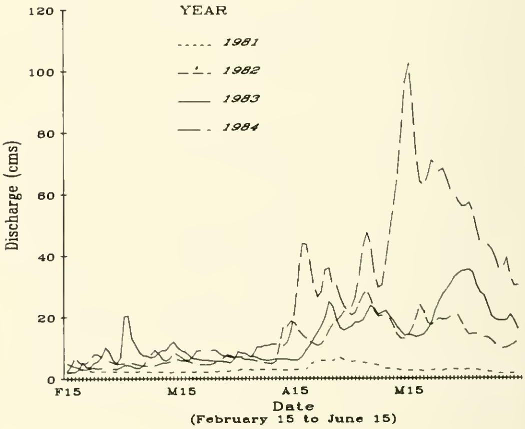

Fig. 3. Stream flow hydrographs for February through 15 June for 1981 through 1984, Salmon Falls Creek, Nevada.

TABLE 1. Average stream width and depth, cutthroat trout weight, population, biomass, and density estimates, and young-adult ratios for Chimney Creek, Nevada, 1981 through 1984.

	Year of sample			
Factor	1981	1982	1983	1984
Mean stream width (m)	1.4	1.4	1.7	2.1
—Std error	0.04	0.04	0.04	0.06
Mean stream depth (m)	0.05	0.05	0.06	0.07
—Std error	0.002	0.002	0.002	0.003
Population size	53	462	420	280
—Std error	0.00	1.38	5.19	2.13
Mean weight (g)	19.2	3.2	7.1	10.4
—Std error	2.29	0.41	0.86	1.47
Biomass (g/m^3)	30.40	37.63	56.09	37.22
—Std error	3.99	5.26	7.31	5.57
(g/m^2)	1.30	1.93	3.26	2.52
—Std error	0.17	0.27	0.42	0.38
Density ($no./m^3$)	1.58	11.80	7.91	3.58
—Std error	0.21	1.65	1.03	0.04
($no./m^2$)	0.07	0.60	0.46	0.24
—Std error	0.01	0.08	0.06	0.04
Young-adult ratio[1]	0	97	85	78

[1] Determined from actual catches, not population estimates.

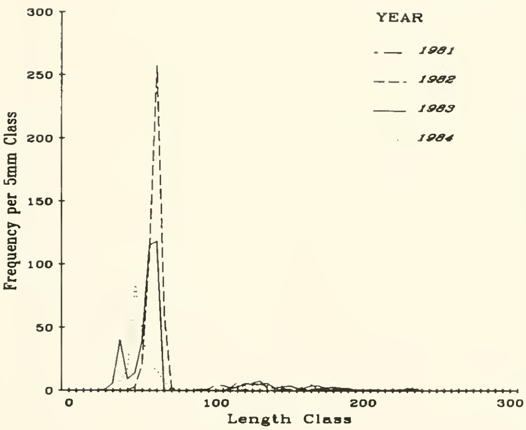

Fig. 4. Cutthroat trout length-frequency distributions from Chimney Creek, Nevada, 1981 through 1984.

simply as the product of mean width, mean depth, and study area length; surface area was length times mean width.

Age and growth factors were determined in conventional fashion. Growth length-weight curves were established using the standard allometric relationship:

$$\text{Log (Weight)} = \text{Constant} + \text{Coefficient} \times \text{Log (Length)}$$

This is arithmetically equivalent to the power function:

$$\text{Weight} = \text{Constant} \times (\text{Length})^{\text{Coefficient}} \qquad (1)$$

For annual comparisons, we have elected to refer to the coefficient in equation (1) as a growth coefficient to avoid confusion with other growth and production factors in the literature. Mean condition (K) was determined using both the isometric relationship (2) and the allometric relationship (3) using the growth coefficient determined in equation (1):

$$K = (10^5 \times \text{Weight})/(\text{Length})^3 \qquad (2)$$

$$K = (10^5 \times \text{Weight})/(\text{Length})^{\text{Coefficient}} \qquad (3)$$

The young-adult ratio (YAR) was computed as the proportion (in percentage) of the population contributed by YOY individuals.

Because actual stream flow data for Chimney Creek were unavailable, we used the flows for nearby Salmon Falls Creek in the Snake River drainage to estimate runoff patterns. To account for possible variations over the area, runoff for upper Mary's River in 1982 was regressed against runoff in Salmon Falls Creek during the same period. Runoff patterns (not absolute flows) were essentially indistinguishable ($R^2 = 0.95$; Fig. 2). Consequently, the hydrographs generated for Salmon Falls Creek for 1981 through 1984 were considered to adequately reflect runoff

TABLE 2. Mean cutthroat trout lengths, weights, and population condition factors and growth factors for Chimney Creek, Nevada, 1981 through 1984[1].

	Year of sample			
Factor	1981	1982	1983	1984
Adult mean length (mm)	127.8	163.6	151.2	154.3
—Std error	4.03	6.57	3.95	4.63
Adult mean weight (g)	19.2	52.2	38.2	43.1
—Std error	2.29	6.03	3.54	4.44
YOY mean length (mm)	—	57.1	50.5	46.2
—Std error	—	0.17	0.47	0.43
YOY mean weight (g)	—	1.9	1.4	0.8
—Std error	—	0.02	0.03	0.03
Mean isometric condition	0.77	1.00	1.01	0.80
—Adult only	0.77	1.13	0.95	0.97
—YOY only	—	1.00	1.02	0.75
Mean allometric condition	0.47	0.56	1.34	0.31
—Adult only	0.47	0.56	1.35	0.30
—YOY only	—	0.56	1.33	0.31
Growth parameters				
—Coefficient	3.10	3.14	2.93	3.23
—Constant	−12.29	−12.10	−11.26	−12.71

[1] Determined from actual catches, not population estimates.

patterns over the geographic region, including Chimney Creek. Mary's River stream flow data were obtained from U.S. Geological Survey water resources data handbooks for Nevada (USDI 1982a, 1985a). Salmon Falls Creek, though larger than Chimney Creek, was selected because we had access to complete flow records in water resources data handbooks for Idaho (USDI 1982b, 1983, 1984, 1985b).

RESULTS

Stream discharge patterns for the spring runoff periods of 1981 through 1984 were extremely variable (Fig. 3). The high peak discharge on 16 May 1984 established a record flow for the 75 years that records have been kept on Salmon Falls Creek (USDI 1985). Although apparently not a record low peak flow, the highest discharge in 1981 (27–28 March) was just 1.9 times greater than the 72-year average discharge (in comparison, the 1983 peak was 26.4 times the average) (USDI 1982, 1985). Conversely, minimum flows were relatively stable throughout the period.

Fish populations in Chimney Creek fluctuated over the period (Table 1) and were at their most depressed levels during the drought year of 1981 and the record runoff of 1984. Most of this difference was due to relatively weak YOY age classes (i.e., low YAR), particularly in 1981 when no YOY individuals were encountered (Fig. 4). In 1982, the YOY class exhibited its greatest strength, while the absolute number of adults was at its lowest point during the study.

Of particular interest, however, is the split YOY class observed in 1983. Two distinct subpopulations (length-classes) of YOY individuals collected in 1983 were separated by an average of approximately 20 mm. This suggests the occurrence of at least two spawning periods. Inspection of the hydrograph from 1983 in Figure 3 reveals one early peak runoff event in late February, followed about six weeks later by the beginning of the expected spring runoff. The runoff pattern after mid-April in 1983 was similar to that of the same period in 1982, except that 1983 reached peak discharge about 1 June, much later than the early May peak of 1982. We do not know whether the first spawn occurred in response to the February peak or as flows began to recede after the initial peak in late April, followed by normal spawning after the true peak discharge in May. Inspection of the sizes of the fish relative to other years (Fig. 4), however, suggests the latter alternative.

Despite the fairly large fluctuations in population size, biomass as a function of average stream volume fluctuated much less. Only 1983 showed an unusually large biomass because of an exceptionally strong YOY age class. Average condition (Table 2) was also high during this period, particularly the allometric value. In general, however, the isometric relationship provided higher estimates of robustness. In fact, allometric estimates were typically very low (assuming an optimum of 1.00), indicating disproportionately more growth in length than in mass. Examination of the growth coefficient emphasizes this different growth performance in 1983, the only year in which average YOY isometric condition exceeded that of adults.

DISCUSSION

Floods have long been considered destructive events for trout populations. Seegrist and Gard (1972) showed flooding to reduce brook trout production in California and indicated that the effect was most severe on adult trout. Similarly, Elwood and Waters (1969) demonstrated impaired brook trout production when flooding reduced invertebrate food supplies. Such results are to be expected for fish residing in typically stable or predictable environments. In fact, the beaver impoundments often used by brook trout might be considered unusually stabilized habitats. It seems likely, however, that trout inhabiting frequently and capriciously flooded environments would be less disturbed by flooding.

Interestingly, 1981, the year with the most stable flows, yielded no YOY individuals in the population sample. Chimney Creek became intermittent in August 1981, and some studies (Lea 1968, Platts 1960) have suggested that downstream migration from natal gravels may occur shortly after emergence, possibly stimulated by receding flows (Benson 1960). The early attenuation of adequate flows may have prompted an early emigration. Coffin (1982), however, states that YOY Humboldt cutthroat remain in their natal stream at least until the following year's runoff period. Given the large adult population and the fact that YOY are normally present in mid-August, it seems more likely that one of two other factors was operating: (1) quality rearing habitat may have become limiting, or (2) adults in Mary's River could not ascend Chimney Creek because low flows were insufficient to allow passage over beaver dams near the confluence of Chimney Creek and Mary's River (Gene Weller, Regional Fisheries Supervisor, Nevada Department of Wildlife, Elko, Nevada, personal communication). In the former case, if rearing habitat were at a premium, YOY individuals would be forced into more frequent, fatal encounters with predatory adults; in short, they may have been heavily preyed upon in 1981. Van Deventer and Platts (in press) showed that YOY survival was quite high in a small stream in Yellowstone National Park from which adults emigrated immediately after spawning, further suggesting that predation may have been a significant factor in Chimney Creek in 1981.

Our results suggest that Humboldt cutthroat trout populations are not severely affected over the long term by even extreme flooding and that appropriate responses to irregular discharge events constitute part of their adaptive strategy. In fact, the somewhat reduced number of YOY in the 1984 sample may have resulted simply from early passive movement downstream and not any actual reduction in productivity. Johnson (1983) suggests that increased flows stimulated downstream movement of Lahontan cutthroat trout in Cold Creek, California, but there is also the possibility that this could be interpreted as a passive downstream movement of YOY individuals in response to periods of increased flow. We have also demonstrated one clear incidence of a split spawning period that produced two distinct YOY subpopulations. We cannot determine precisely the triggering mechanism for this behavior but offer two alternative hypotheses. First is that the early discharge event in the first part of March initiated an early spawning run. Second is that the undulating nature of the main portion of the discharge hydrograph (mid-April to mid-June) was perceived by spawners to be two distinct runoff events. Because of the parity in length of the principal 1983 YOY subpopulation with that of 1982, we consider the latter alternative more probable. Smith (1941) reported split runs of Yellowstone cutthroat (*S. c. bouveri*) in two tributaries of Yellowstone Lake, which he attributed to genetic differences between two distinct subpopulations of spawners. We believe a similar mechanism may be at work in Chimney Creek. This could take the form of either two distinct subpopulations ascending from Mary's River at different times or out-of-phase spawning between migratory and resident populations. There is little basis at this point for deciding which of these is more likely, and it is easy to imagine migratory individuals in a river environment responding to watershed events differently than small tributary residents might. Migratory individuals would be responding to watershed-wide (macro) events, whereas behavior of tributary residents would be triggered by local (micro) events. More sophisticated studies of spawning movement and behavior, and more localized discharge data are needed to better understand this apparently adaptive behavior.

Whichever mechanism is responsible for promoting two subpopulations of spawners, the adaptive advantage is clear: sufficient genetic diversity is present to ensure successful reproduction during the most irregular of weather patterns. Judging by the very high average condition of both trout age groups in 1983, it seems also to confer the ability to exploit unusually favorable conditions (which must have occurred in 1983 to promote high population sizes and high robustness). That the trait may be a primitive one is corroborated by its occurrence in the genetically distant Yellowstone subspecies. Loudenslager and Gall (1980) have shown Lahontan cutthroat trout to be the most genetically diverse of the subspecies. In fact, splitting the Lahontan into Lahontan and Humboldt subspecies would produce two subspecies of unusually high genetic diversity, with the Humboldt strain apparently the more variable. This quite strongly suggests the value of maintaining a variable gene pool to promote environmental tolerance in a capricious environment.

As cold-water fisheries in the interior western United States continue to increase in value, and as the value of preserving biological diversity becomes more widely recognized, we hope that preliminary efforts such as this will stimulate further research into mechanisms of adaptation to apparently unfavorable habitat conditions. The fact that Humboldt cutthroat trout can persist and even prosper in water unsuitable to brook and rainbow trouts has already been demonstrated (Behnke 1979, Platts and Nelson 1983). Many interior watersheds in the western United States are presently degraded from inappropriate land-use practices, and it seems clear that tolerant salmonids such as the Humboldt cutthroat could provide a valuable resource for stocking into habitats generally deemed unsuitable for trout. This could be an adjunct treatment for increasing the fishery resource of the degraded streams common in overgrazed watersheds in the Intermountain and Great Basin areas. It should be considered only as an interim step while more permanent rehabilitation efforts aimed at restoring streams to their native potential are instituted.

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NICHE PATTERN IN A GREAT BASIN RODENT FAUNA

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ABSTRACT.—Niche pattern of a desert rodent community in shrub habitats of central Utah was examined in the canonical space formed by the first four principal components of trapsite microhabitat. Positions of species centroids differed significantly ($P < .05$) in this space and were consistent with the known habits of each; thus, it appears that the principal components measured biologically meaningful facts. Abundance in optimal habitat (a_i) increased with niche breadth (v_i) and decreased with increasing difference of centroids of a species from the overall mean habitat (d_i). v_i was positively related to d_i. Differences between niche pattern of this community and that of deciduous forest small mammals are discussed.

Identification of mechanisms that prevent competitive exclusion has been the objective of many studies of rodent habitat. Habitat selection is reported to be a major mechanism allowing sympatric coexistence of cricetid rodents (Grant 1972, M'Closkey and Fieldwick 1975, Dueser and Shugart 1978, Kitchings and Levy 1981, Van Horne 1982, Parren and Capen 1985, Seagle 1985b). Heteromyid rodents reportedly partition foraging space on the basis of microhabitat (Lemen and Rosenzweig 1978, Price 1978, M'Closkey 1980, Hallett 1982, Thompson 1982a, 1982b, Price and Brown 1983). Research into other aspects of community structure such as relationships between abundance and niche parameters has recently received attention (Dueser and Shugart 1979, Anthony et al. 1981, Carnes and Slade 1982, Van Horne and Ford 1982, Seagle 1985a, 1985b, Seagle and McCracken 1986), but an understanding of these complex interactions is lacking.

The interrelationship between abundance, niche breadth, and niche position is called niche pattern (Shugart and Patten 1972). Niche pattern has not been studied in enough communities, nor long enough in any one community, to understand how individual components are related or how they vary with other factors such as community stability and productivity. In communities that have been studied (birds by Shugart and Patten 1972, eastern deciduous forest small mammals by Dueser and Shugart 1979, Seagle 1985b, Seagle and McCracken 1986), the most abundant species had the broadest niches and were closest to the mean habitat.

To evaluate general relationships among abundance in optimal habitat, niche position, and niche breadth, and to identify factors that may influence these relationships (and thus affect community structure), it is necessary that a wide variety of communities be studied. The objectives of this paper are: (1) to describe the niche pattern of a rodent community in shrub habitats of the Great Basin Desert and (2) to compare the observed niche pattern with that reported for deciduous forest rodents (Dueser and Shugart 1979) in an attempt to identify factors related to differences in structure of these two communities.

STUDY AREA AND METHODS

Study Area

Shrub communities in the cold desert of central Utah were chosen in Juab and Tooele counties to provide a variety of vegetation and soil characteristics. Some sites were selected on vegetated sand dunes and others in adjacent areas with finer-textured soils. Dominant shrubs on the sandy areas were greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus* spp.), while sagebrush (*Artemisia tridentata*) was dominant on the finer-textured soils. Cheatgrass (*Bromus tectorum*) was the most common herbaceous species, although ricegrass (*Oryzopsis hymenoides*) was locally common on the dunes. The most frequently encountered forbs were Russian thistle (*Salsola kali*) and scurfpea (*Psoralea tenuiflora*) on predominantly sandy soils and *Lepidium* spp. and *Descurania* sp. on finer-textured soils.

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Trapping

Small mammals were trapped with museum special snap traps baited with oatmeal and placed 12–15 m apart in 4–10 parallel transects of 10–25 traps each. Transects were trapped for three consecutive nights. Traps were usually baited in the afternoon and remained set through each trapping period. Captured animals were removed from traps each morning and the capture site, species, sex, and age of each recorded.

Microhabitat Variables

Nine variables were used to characterize microhabitat at each trapsite. These variables included percent bare ground and litter, shrub, grass, annual, and total vegetative cover. Cover variables were visually estimated in a 1-m^2 circular plot centered on each trapsite. Distance from the trap to the nearest shrub and the height of that shrub were measured. Soil texture was classified as either sand or fines (silt and clay). Bowers (1979) used similar variables to characterize habitats of desert rodents in Nevada.

Analysis

Symbolism for niche pattern parameters follows Dueser and Shugart (1979). d_i, a measure of niche position, represents the distance from the habitat mean to the centroid of species i. Niche breadth is symbolized by v_i. The abundance of species i in its optimal microhabitat is represented by a_i.

Parameters of niche pattern were estimated following a modification of the methods of Dueser and Shugart (1979). Dueser and Shugart used discriminant function analysis (DFA) to reduce intercorrelations among the original microhabitat variables and obtain a more parsimonious space in which to examine niches. We used principal component analysis (PCA) to achieve the same goal because: (1) the normalized eigenvectors provide an orthogonal basis for the reduced space; and (2) the method requires no distributional assumption, whereas DFA requires the variance/covariance matrices of all species to be equal, thus implying niches of the same size and shape. Because habitat variables were in different units (i.e., cm, %), a correlation matrix was used instead of the variance/covariance matrix in calculation of the principal components.

Table 1. Principal components of trapsite habitat.

	Normalized eigenvectors			
Variable	PC1	PC2	PC3	PC4
Litter cover	0.1319	0.4783	0.3762	0.3222
Annual cover	.48797	−.2532	−.0521	−.1255
Shrub cover	.1130	.6223	−.0303	.0984
Grass cover	.4484	−.3152	−.0560	.0494
Shrub height	.0231	.2232	.4206	−.8156
Distance to shrub	.160	−.1911	.5937	.4347
Bare ground	−.5087	−.1641	−.0658	−.0729
Substrate	.0006	−.3186	.5610	−.0796
Vegetative cover	.5207	.0767	−.0570	−.0495
Eigenvalue	3.448	1.826	1.329	.920
% of variance	23	20	15	10
Cumulative %	38	58	73	83

Relative positions and separation of centroids of a species in PC-space were examined to determine if the principal components measured biologically relevant facts. Capture and noncapture sites of each species were compared with univariate (ANOVA) and multivariate (MANOVA) analysis of variance to detect species that did not respond to the habitat variables and to determine the relevance of the PCA-generated variables. Because many noncapture sites were probably within the habitat of each species, these tests should be conservative estimates of microhabitat use. Equality of centroids of a species was tested with MANOVA. Test statistics with $P < .05$ were considered significant. d_i was estimated as the Euclidean distance from the mean of species i's capture sites to the mean of all microhabitats included in the analysis. These microhabitats included all capture and noncapture trapsites that were measured. Including only capture sites forces the centroids of abundant species toward the origin (Carnes and Slade 1982). When all trapsites are included, there is no a priori reason for species with high a_i to have low d_i.

Niche breadth (v_i) was estimated as the mean square distance from the capture points of species i to its centroid (Carnes and Slade 1982). This measure of breadth is independent of distance from origin and niche orientation, while the coefficient of variation of Dueser and Shugart's d-bar is not.

The product of the number captured (n_i) and $(2\pi\sigma^2)^{-\frac{1}{2}}$ (Dueser and Shugart 1979) was used as an estimate of a_i. Sigma-squared was

TABLE 2. Means of principal components at capture and noncapture sites of each species. DO = *D. ordii*, PP = *P. parvus*, PM = *P. maniculatus*, RM = *R. megalotis*, OL = *O. leucogaster*, AL = *A. leucurus*, EM = *E. minimus*.

		PC1		PC2		PC3		PC4		Wilk's
Species	N	Cap	Noncap	Cap	Noncap	Cap	Noncap	Cap	Noncap	Lambda
DO	40	−1.12[a]	−0.50	−0.34	−0.06	0.45[b]	0.04	−0.06	0.06	0.9770[a]
PP	26	−.82	−.52	.43[b]	−.10	−.39[b]	.08	.09	.05	.9880
PM	107	−.94[a]	−.46	.38[a]	−.16	.18	.04	−.15[b]	.09	.9581[a]
RM	18	−.33	−.54	.65[b]	−.10	.18	.06	−.27	.06	.9880
OL	8	−1.03	−.53	.35	−.08	.76	.05	−.04	.05	.9930
AL	5	−.61	−.53	.96[b]	−.09	.55	.05	.28	.05	.9920
EM	7	−.27	−.54	.51	−.08	−.37	.06	.06	.05	.9972

[a] P < .01
[b] P < .05.

estimated by $v_i\ (n_i/(n_i - 1))$. The calculation of a_i assumes that all species were censused equally and that n_i is representative of the density of species i for all i (Dueser and Shugart 1979). Because this assumption is questionable for this study, a_i should be treated as an approximate index of the height of the resource utilization curve. Relationships between a_i, d_i, and v_i were examined both graphically and with multiple regression.

RESULTS AND DISCUSSION

Capture Results

Three hundred eighty-five small mammals were captured during 3,364 trapnights on 17 study plots. Microhabitat was measured at 47% (725) of the 1,538 trapsites, which included 211 capture sites. These captures were composed primarily of *Peromyscus maniculatus* (n = 107, 51%), *Dipodomys ordii* (n = 40, 19%), *Perognathus parvus* (n = 26, 12%), *Reithrodontomys megalotis* (n = 18, 9%) *Onychomys leucogaster* (n = 8, 4%), *Eutamias minimus* (n = 7, 3%), and *Ammospermophilus leucurus* (n = 5, 2%). Other species captured included *Dipodomys microps*, *Microdipodops megacephalus*, *Perognathus formosus*, *Peromyscus truei*, *Lagurus curtatus*, *Microtus montanus*, and *Sorex cinereus*.

Principal Components

The first component (PC1) accounted for 38% of the "variation" in the data and was weighted positively on annual, grass, and total vegetative cover, and negatively on bare ground (Table 1). This component can be interpreted as herbaceous cover. The second component (PC2) was largely influenced by shrub and litter cover and accounted for 20% of the "variation." The third component (PC3) accounted for 15% of the "variation" and was strongly related to shrub height, distance to nearest shrub (a decreasing function of shrub density), and soil texture. This component increased as shrubs became taller and more sparse and soils became more sandy. Component 4 (PC4) represented a contrast between shrub height and distance to nearest shrub. This component increased with increasing sparseness of shrubs and decreasing shrub height and can be interpreted as openness. Together, the first four components accounted for 83% of the variation in the original nine variables. Niche pattern was examined in the four-space determined by these components.

Capture vs. Noncapture Sites

The mean of *Peromyscus maniculatus* capture sites was significantly less on PC1 and PC4 and significantly greater on PC2 than the mean of noncapture sites (ANOVA, Table 2). Capture sites had taller shrubs, more shrub and litter cover, and less annual cover. Differences were significant in MANOVA.

Dipodomys ordii capture and noncapture sites differed significantly (MANOVA, Table 2). PC1 was significantly less and PC3 significantly greater on capture sites. These differences indicate *D. ordii* was captured more often in microhabitats with less annual and shrub cover, but with tall, low-density shrubs.

Capture sites of *Perognathus parvus* were in areas of finer soil texture with denser shrubs, greater shrub and litter cover, and less annual cover than noncapture sites. Although capture sites were significantly

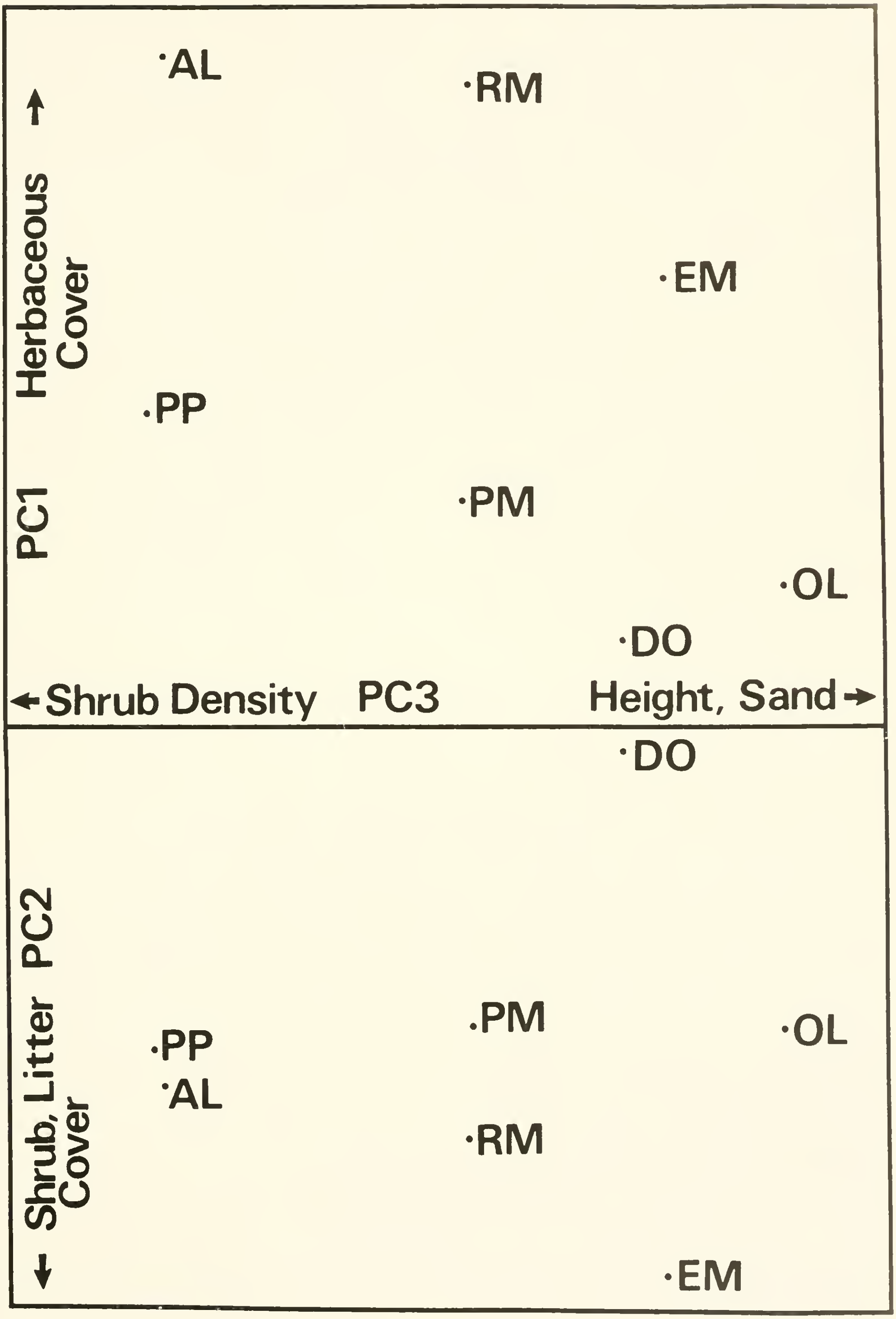

Fig. 1. Means of principal components at capture sites of each species. Symbols: DO = *D. ordii*, PP = *P. parvus*, PM = *P. maniculatus*, RM = *R. megalotis*, OL = *O. leucogaster*, AL = *A. leucurus*, EM = *E. minimus*.

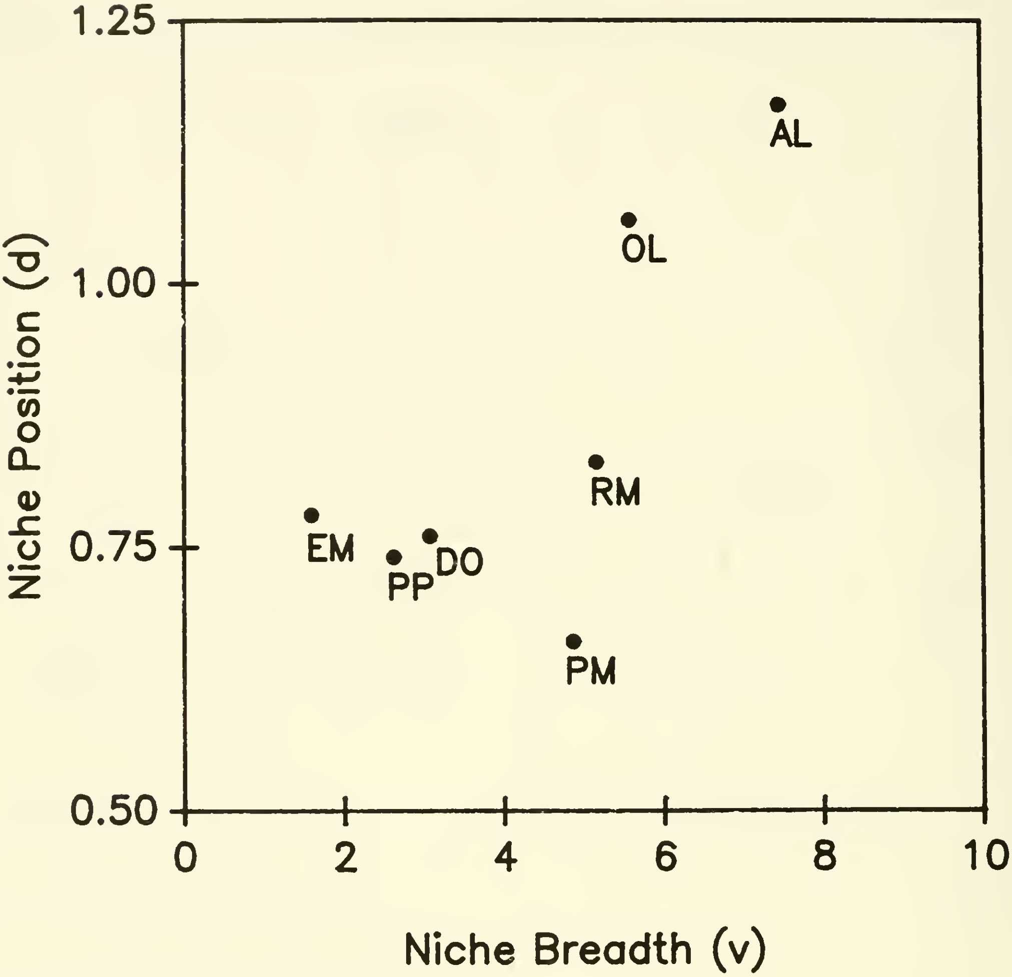

Fig. 2. Relationship of niche position to niche breadth. Symbols are same as in Figure 1.

greater on PC2 and significantly less on PC3 (ANOVA), the differences were not significant when PC1–PC4 were considered simultaneously (MANOVA, P = .070).

PC2 scores of capture sites of *Reithrodontomys megalotis* were significantly greater than those of noncapture sites. Capture sites of *R. megalotis* were characterized by high annual, shrub, and litter cover with tall shrubs. The difference between capture and noncapture sites was not significant in MANOVA (P = .069).

Capture sites of *Onychomys leucogaster*, *Ammospermophilus leucurus*, and *Eutamias minimus* did not differ significantly from noncapture sites along PC1–PC4 (MANOVA). The lack of significance may be due to the low number of captures for each of these species, although for *O. leucogaster* it may be due to nomadic behavior and broad habitat affinities. *Onychomys leucogaster* and *A. leucurus* were captured more often on sandy soil with tall, relatively dense shrubs and less cover by annuals (Table 2). The high mean value of PC4 for *A. leucurus* is due to a very high litter cover. Capture sites of *E. minimus* had more annual cover and finer soil texture than noncapture sites. The high score on PC2 is due to high litter and not to shrub cover.

Differences Among Species

Means of species capture sites differed significantly along PC1–PC3 (MANOVA, Fig. 1). Species differed significantly along PC3. Capture sites of *A. leucurus* and *P. parvus* are low on PC3, indicating habitats with dense, short shrubs and fine soil texture. The means of capture sites of *D. ordii* and *O. leucogaster* are on the high end of the PC3 scale. These species were captured most often on sandy soil with tall, sparse shrubs. The positions of *E. minimus*, *O. leucogaster*, and *D. ordii* are distinctly but not significantly separated along PC2. Capture sites of *D. ordii* had lower shrub and litter cover, while those of *E. minimus* were high in these attributes. Differences between species along PC1 were not significant. Species not separated along PC2, however, have large differences along PC1. Both *A. leucurus* and *R. megalotis* were found in greater herbaceous cover than *P. parvus* and *P. maniculatus*.

Dipodomys ordii utilized relatively open areas (Jorgensen and Hayward 1965, Rosenzweig 1973, Schroder and Rosenzweig 1975, Brown and Lieberman 1973); however, *P. parvus* inhabited more closed, shrubby areas (Rosenzweig and Winakur 1969, Rosenzweig 1973, Nichols et al. 1975, Fautin 1946). Although found on nearly every grid, capture sites of *P. maniculatus* were closer than noncapture sites to tall shrubs. This agrees with results of Fautin (1946) and Rosenzweig and Winakur (1969). Location of *R. megalotis* capture sites in dense vegetation near large shrubs also agrees with reports in the literature for this species (Fautin 1946, Rosenzweig and Winakur 1969). Based on differences of means for a species in PC-space and consistency of habitat descriptions with published accounts for each species, it appears that the principal components represented habitat structure relevant to the habitat utilization of each species.

Niche Pattern

Niche breadth increases with distance from mean habitat (Fig. 2). *Eutamias minimus*, *P. parvus*, and *D. ordii* had the narrowest niches, while *R. megalotis*, *O. leucogaster*, and *A. leucurus* had the broadest. *Peromyscus maniculatus*, *P. parvus*, and *D. ordii* were nearest the mean habitat, while *O. leucogaster* and *A. leucurus* were the most distant. Although the more numerous species had low d_i, the less numerous species did not all have high d_i. Abundance in optimal habitat decreased with increasing d_i, and, although not as clearly, abundance also decreased with increasing niche breadth (Figs. 3 and 4). Abundant species were close to the mean habitat and had narrower niche breadths. A regression of a_i on d_i and v_i showed a significant linear relationship (F = 8.06, d.f. = 2,4).

This differs from the pattern observed for deciduous forest small mammals (Dueser and Shugart 1979). In the deciduous forest community, the more abundant species of small mammals were close to the mean habitat and had high niche breadths (a_i increased with v_i and decreased with d_i). Differences between results in Dueser and Shugart (1979) and this study may be partly due to different methods of calculating niche metrics. Since the niche metric calculations of Dueser and Shugart (1979) are not correct statistically (Carnes and Slade 1982, Van Horne and Ford 1982), modified methods proposed by Carnes and Slade (1982) were used in this study. However, differences in results may be due to real differences in the two communities.

Species diversity can influence niche breadth. In the desert shrub fauna we primarily worked with 7 species (14 total) as opposed to 4 species in Dueser and Shugart's (1979) deciduous forest. In addition to more species in the desert, the potential niche space may be less since forests are structurally more complex. Microhabitat niches of desert rodents must be narrower or overlap more than those of forest small mammals. In light of extensive literature on habitat partitioning in desert rodents (Bowers 1979, Holbrook 1979, Price 1978, Wondolleck 1978, Rosenzweig 1973, Thompson 1982a, 1982b, Hallett 1982, Price and Brown 1983, Lemen and Rosenzweig 1978, etc.), higher overlap is improbable, and we suggest narrower niche width as the most likely situation.

Frequency of occurrence or availability of a habitat in a given area decreases with increasing difference from the mean habitat (Shugart and Patten 1972). A species whose habitat centroid is far from the overall mean may either remain in a small, infrequent habitat patch or move between patches. A population, on the other hand, requires a minimum size or, equivalently, a minimum area to maintain itself. A species with high d_i should be broad-niched because: (1) in the course of its daily movements an individual is likely to move through several small patches of different types (fine-grained generalist); or (2) each individual remains in a single habitat patch

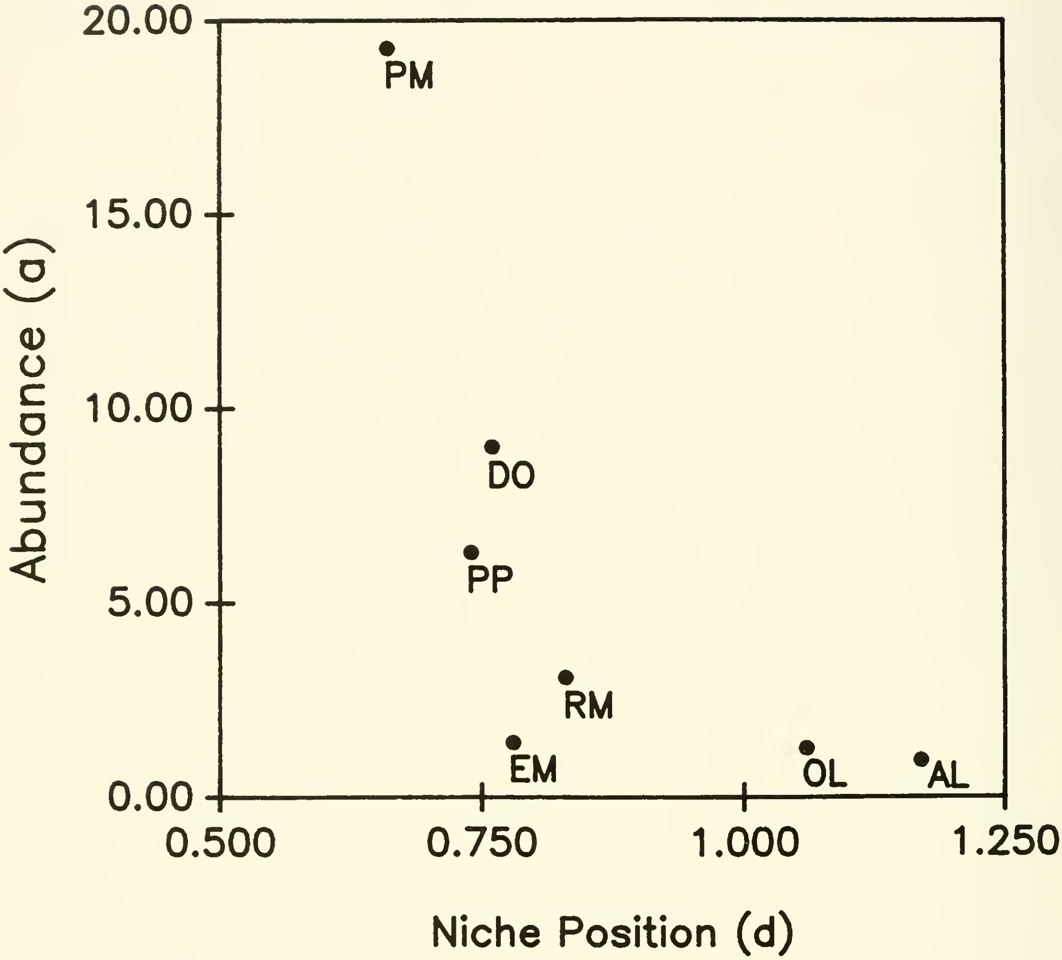

Fig. 3. Relationship of abundance to niche position. Symbols are same as in Figure 1.

type, but, because distant (high d_i) patch types are rare, different individuals are in different patch types. There remains the possibility of a species specializing on one rare patch type (high d_i, low v_i). These species should be highly mobile and relatively rare.

Species packing in common habitats and generalizing in rare habitats could explain the observed pattern of abundant, narrow-niched species with low d_i and less abundant, broad-niched species with high d_i; but another possible factor is temporal stability in habitat structure. In postburn or postdisturbance succession, the structure of desert shrub habitats is relatively more stable than that of forests. Clearly, a burn changes habitat structure and faunal composition of both (Kozlowski and Ahlgren 1974), but the forest is changed more drastically and also will show greater changes in 100 yr (even 15 yr). The relative stability of desert structure could allow increased habitat specialization of dominant species (Ricklefs 1979).

Our data fit Rosenzweig's (1974, Lemen and Rosenzweig 1978) theory of evolution of habitat selection. Rosenzweig theorized that if habitat patch types are not equally abundant, there exists the possibility for two successful coexisting phenotypes, the specialist from the abundant patch type, and the generalist who can best exploit the mixture of patch types. The more common species (high a_i) of this study were in the more abundant habitats (low d_i) and had relatively narrow niches, while low a_i species were in less abundant habitats (high d_i) and had broader niches. The

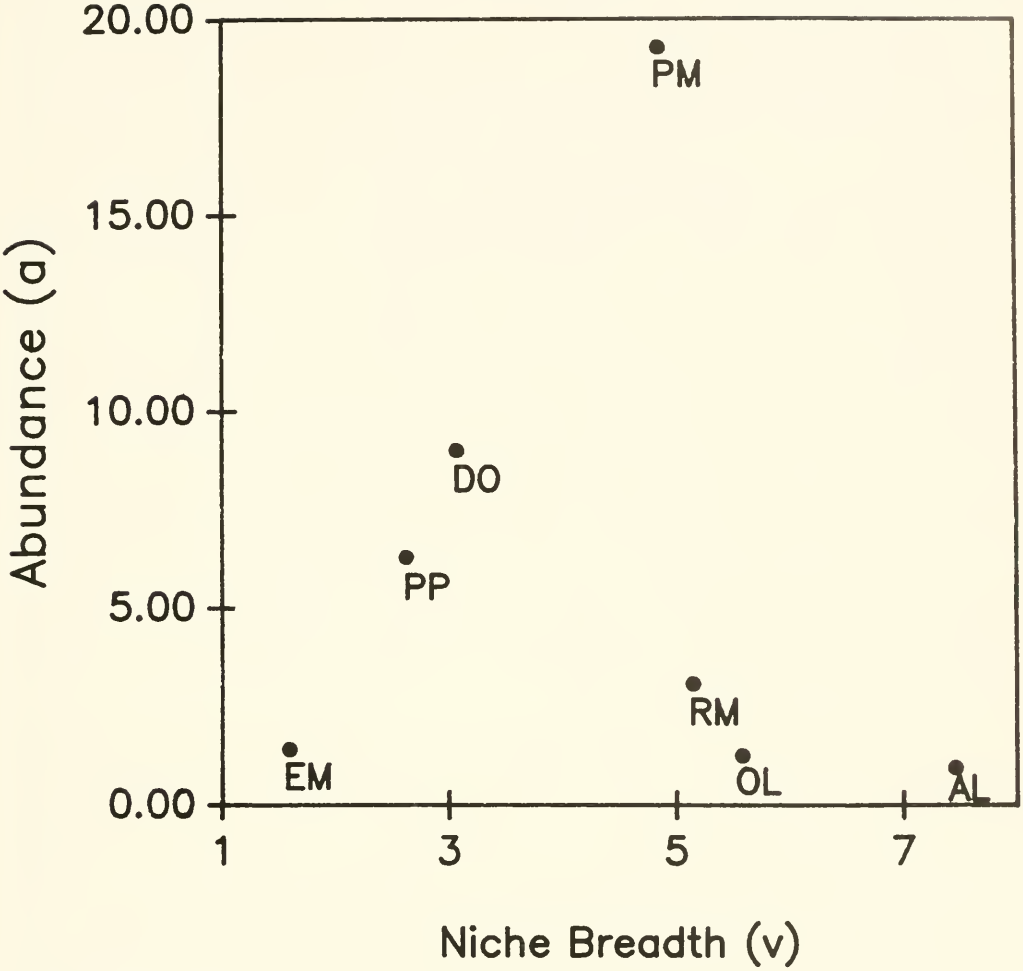

Fig. 4. Relationship of abundance to niche breadth. Symbols are same as in Figure 1.

species in the desert rodent community of this study differed in microhabitat preferences. It appears that there are a few abundant microhabitat "patch types," each with its own specialist. The generalists are using a wider variety of patches, although the patch types used by each may differ.

The differences in niche pattern of deciduous forest and desert small mammal communities point to different factors influencing the community structure of each. Species diversity, stability and diversity of habitat structure, and possibly many other factors influence niche characteristics of species in each community, affecting in turn species evenness, local distribution, and perhaps the nature of competitive interactions. More studies of various communities and a standardization of techniques are necessary for the concept of niche pattern to help identify these factors and elucidate the importance of each.

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PLANTING DEPTH OF 'HOBBLE CREEK' MOUNTAIN BIG SAGEBRUSH SEED

Tracy L. C. Jacobson[1] and Bruce L. Welch[1]

ABSTRACT.—We conducted a greenhouse study in which 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seeds were planted at various depths in soil to determine the optimal planting depth. Results showed that the optimal planting depth is 5 mm or less.

Big sagebrush (*Artemisia tridentata*) is an important winter forage for wintering mule deer (*Odocoileus hemionus hemionus*) in the Rocky Mountains. In some areas big sagebrush is the single most important mule deer winter forage (Smith 1950, Leach 1956, Kufeld et al. 1973). This is due to big sagebrush abundance, availability, and superior winter nutrient content (Welch 1983). Recent reports have shown significant variation among subspecies and accessions within subspecies for production, preference, and winter nutrient content (Scholl et al. 1977, McArthur et al. 1979, Sheehy and Winward 1981, Welch and Pederson 1981, Welch et al. 1986, Personius et al. 1987, Wambolt et al. 1987). Of the accessions tested, an accession of subspecies *vaseyana* called 'Hobble Creek' was found to be the most preferred accession by wintering mule deer and among the most preferred accessions by wintering domestic sheep (*Ovis aries*) (Welch et al. 1986). A. Perry Plummer discovered it in 1968 at the mouth of Hobble Creek drainage just east of Springville, Utah. 'Hobble Creek' is a low-elevation mountain big sagebrush whose forage value exceeds most winter forages for crude protein, phosphorus, carotene, and digestibility (Welch et al. 1986) and does not contain substances that lower grass cell wall digestion in ruminant animals (Hobbs et al. 1986). 'Hobble Creek' is needed to increase the nutrient content of winter diets of mule deer and domestic sheep.

'Hobble Creek' can be established by direct seeding, by transplanting bareroot or containerized stock, and by a technique called "mother plant" (Welch et al. 1986).

Direct seeding is the most practical method for establishing this superior accession of big sagebrush. Factors that affect germination and establishment include light, temperature, available moisture, seed quality, seedbed preparation, seeding mixture, competition reduction, planting time, and planting depth (Goodwin 1956, Payne 1957, Weldon et al. 1959, Deitschman 1974, McDonough and Harness 1974, Harvey 1981). The last factor, planting depth, is the subject of this study. This study was designed to determine the optimal planting depth for seedling emergence and the effects of stratification on emergence.

MATERIALS AND METHODS

The planting depths evaluated in this study were surface, 2 mm, 5 mm, 10 mm, and 15 mm. The depths were compared by planting unstratified seeds and stratified seeds. Petri dishes were also sown with seeds to check seed viability.

Seeds were collected in November from a breeder plot in Hobble Creek Canyon east of Springville, Utah. Entire inflorescences were clipped, bagged, and air dried at room temperature for two weeks. Large stems were separated from the seed and chaff by hand stripping. After stripping, the seed and chaff were passed through a series of screens that removed the fine stems and larger particles of chaff. The seed was cleaned to 70% purity with an air flow seed cleaner. At the time of use, a dissecting scope and tweezers were used to remove abnormal seeds and remaining chaff. The unstratified seeds were sealed in glass vials and stored at room temperature. The seeds to be stratified were treated with a fungicide (1 gram fungicide to 1 liter distilled water), sown in 9-cm sterile petri dishes containing distilled water–saturated no. 4 Whatman filter pads[2], and then placed in a cooled room (2 C) for 10 days (Deitschman 1974).

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The experimental design consisted of 12 treatments (stratified + unstratified and control + 5 planting depths) with 5 replications. Sixty containers were randomly arranged on a greenhouse bench. Ten of the 60 containers were sterile 9-cm petri dishes (controls), and 50 were 6-inch-deep by 2-inch-square pots. The petri dishes contained two layers of no. 4 Whatman filter papers. The square pots contained a sterile sandy loam that had been watered and compacted to the desired depth before the seeds were sown. Soil was placed over the seeds in such a manner to maintain the desired depth and to eliminate compaction. Fifteen 'Hobble Creek' big sagebrush seeds were sown in each container. Each of the six treatments was run on stratified and unstratified seeds (control, petri dishes, surface, 2 mm, 5 mm, 10 mm, and 15 mm).

Seedlings were grown for five weeks. Day length was extended to 12 hours with the use of fluorescent lighting. Temperature was maintained between 15 and 10 C both day and night. Pots were checked daily for germinated seeds, and twice a day pots were watered with distilled water, using a squeeze bottle to avoid disturbing the soil surface. Germination or emergence was classified as complete with the appearance of green-colored cotelydons. T-tests were used to detect significant differences between stratified and unstratified seed for the various planting depths. Analysis of variance was used to determine significant differences among the planting depths (Ryan et al. 1976).

RESULTS AND DISCUSSION

Results of this study are given in Tables 1 and 2. Stratification treatment stimulated significantly (5% level) the rate and number of seeds emerged (Table 1). Stratified seeds started emerging three days after planting, while unstratified seeds did not emerge until seven days after planting. Stratified seeds had a significantly higher number of seeds emerging for surface, 2-mm, and 5-mm depth than unstratified seed. Stratification had no significant effect on the number of seed emerging for control (petri dishes) and at the 15-mm depth. Unstratified seed had significantly more seeds emerge at the 10-mm depth than stratified seed. This last observation could be an artifact of the experiment. Because big sagebrush seeds are released in the late fall or early winter period, these seeds lay on or near the soil surface. During this period and into the spring, the seeds are usually in a moist-cold environment. We believe that the stratified seeds of this study are behaving more like those in nature than the unstratified seeds.

TABLE 1. Comparisons between stratified and unstratified seeds of 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) planted at various depths. Comparisons were made with unpaired t-test. Data are expressed as numbers of seeds germinating out of a possible 75 seeds.

Depth	Seed treatment Stratified	 Unstratified	T-values
	Seeds germinated out of 75		
Petri dishes (control)	63	69	1.897
Surface	48	35	2.982*
2 mm	49	27	2.678*
5 mm	45	33	3.539*
10 mm	0	9	3.087*
15 mm	0	2	1.000

*Significantly different at t = 0.05, 5 d.f. = 2.015.

Because of the significant effects of stratification, the data collected from stratified and unstratified seeds were not pooled for the analysis of variance. Analysis of variance did detect significant difference for numbers of seeds emerging at the various depths (Table 2). Controls (petri dishes), both stratified and unstratified, produced significantly (P = .05) more seedlings than all five depths. Surface, 2-mm, and 5-mm depths of both stratified and unstratified seeds produced significantly more seedlings than 10-mm or 15-mm depths.

The probable higher temperatures and relative humidity in the petri dishes may be the reasons that more seedlings were produced in the dishes, compared with the number produced on the surface. We therefore conclude that 'Hobble Creek' mountain big sagebrush

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[2] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

TABLE 2. Optimal planting depth of 'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) stratified and unstratified seeds. Data are expressed as a mean and standard deviation per depth for five pots containing 15 seeds per pot.

	Seed treatment	
Depth	Stratified Seeds germinated	Unstratified Seeds germinated
Petri dishes (control)	12.6 ± 1.02^{a1}	13.8 ± 0.75^{a}
Surface	9.6 ± 1.50^{b}	7.0 ± 0.89^{b}
2 mm	9.8 ± 0.81^{b}	5.4 ± 3.01^{b}
5 mm	9.0 ± 0.89^{b}	6.6 ± 1.10^{b}
10 mm	0.0 ± 0.00^{c}	1.8 ± 1.17^{c}
15 mm	0.0 ± 0.00^{c}	0.4 ± 0.80^{c}

[1] Means sharing the same superscript within a seed treatment are not significantly different at the 5% level.

should not be planted any deeper than 5 mm and that surface sowing onto disturbed soil is a practical seeding procedure for establishment of this accession (Kelsey 1986, Young and Evans 1986).

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ANNOTATED INVENTORY OF INVERTEBRATE POPULATIONS OF AN ALPINE LAKE AND STREAM CHAIN IN COLORADO[1]

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ABSTRACT.—Benthic macroinvertebrates were collected during the ice-free season (1 July–20 October) over a five-year period from a chain of alpine lakes and intervening streams in the Green Lakes Valley (3,347–3,615 m) in Boulder County, Colorado. A list of taxa was developed for 1981 and 1982, with taxonomic additions for 1983–1985 and comments on community structure, seasonal and elevational changes in species abundance, and noteworthy occurrences. A total of 111 taxa was collected, of which 84% occurred in streams, 58% being exclusively lotic. Dipterans composed 73–81% of total abundance in streams. The littoral benthic zone of lakes was predominantly trichopterans and dipterans, 44–60% and 24–39%, respectively. Numerically important organisms in various lakes and streams were chironomids, simuliids (particularly *Metacnephia*), oligochaetes, and the bivalve *Pisidium casertanum*. An isolated lake and its outlet stream, with unique characteristics, were the sole locations of *Gammarus lacustris* (Amphipoda) and *Glossiphonia complanata* (Hirudinea). Manipulated lowering of a lake along the main drainage exposed abundant and luxuriant colonies of the bryozoan *Fredericella sultana*. This organism was found on 43% of all rocks sampled, a preponderance heretofore unknown for this, or any, ectoproct in alpine or arctic lakes.

There are few studies of lake chains and their intervening streams for mountainous subalpine regions of the world, and, to our knowledge, there are no such studies for true alpine environments. A general review of relevant published information for Colorado, temperate and subarctic North America, and other continents is given by Bushnell et al. (1982).

We obtained information during an extended study of the aquatic macroinvertebrates of an alpine drainage system in the Colorado Rocky Mountains. During the ice-free season, macroinvertebrates were collected from five of six small lakes, and their intervening streams, in the Green Lakes Valley on the eastern slope of the Continental Divide, Boulder County, Colorado.

This paper is a taxonomic inventory for 1981 and 1982, with additional new data for later years (Chironomidae excluded). Annotations are given on seasonal changes in species abundance, elevational aspects of community structure and abundance, and noteworthy occurrences.

The only directly applicable information on the macroinvertebrates of the Green Lakes drainage is by Elgmork and Saether (1970) and Saether (1970), and it is solely for the streams. These publications discuss taxonomic identifications derived from stream collections made in July 1960. Other publications providing information on a variety of environmental topics are those of Halfpenny (1982), Caine (1984), Bushnell et al. (1984), Bushnell and Butler (1984), Caine et al. (1983), Hoffman et al. (1985), Short et al. (1983), Toetz (1985), and Toetz and Windell (1984).

SITE DESCRIPTION: GREEN LAKES DRAINAGE

The glacially carved Green Lakes Valley is about 40° N latitude and has been closed to the public since 1927 by the City of Boulder because the drainage is a municipal water source (Windell and Foster 1982). The entire study area (Fig. 1) lies above timberline in a 5.46-km^2 drainage basin, of which 0.42 km^2 is occupied by the five Green Lakes (GLs 1–5) and Lake Albion (Caine 1982). GL 5, fed by a stream from the Arikaree Glacier, is the highest lake (3,615 m) and is confluent with GL 4 (3,554 m; Fig. 2) via a connecting stream. The streams were named according to the lake from which they emanate; e.g., Stream 5 leaves GL 5 and flows into GL 4; Stream 2 leaves GL 2 and flows into Lake Albion. Lake Albion (3,347 m) is the lowest lake in the study area, and the greatest eleva-

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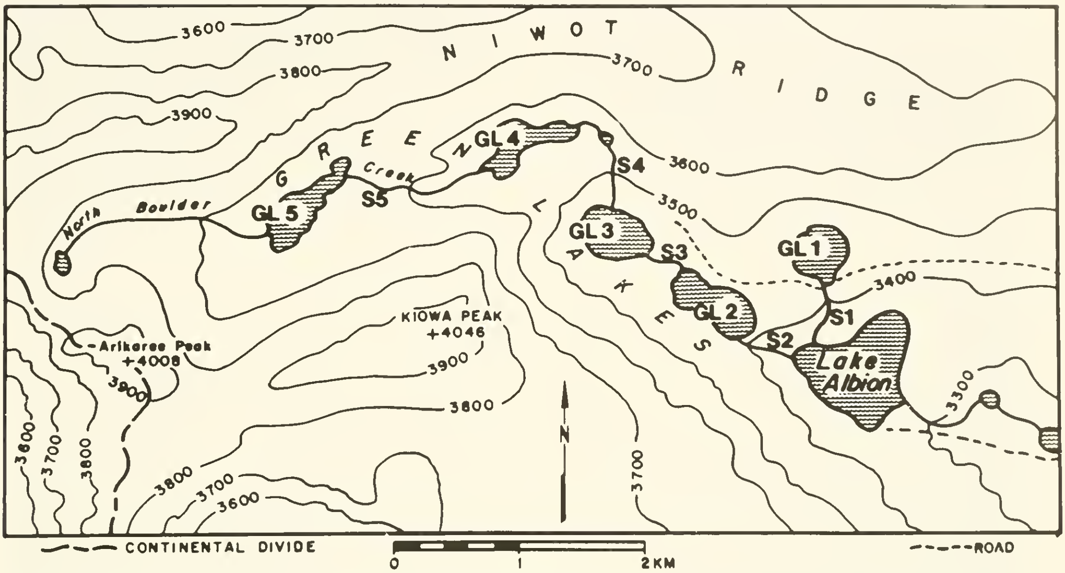

Fig. 1. The Green Lakes (GLs 1–5), Lake Albion, and intervening stream segments of North Boulder Creek (Ss 1–5) located in an alpine valley on the east slope of the continental divide, 42 km west of the city of Boulder, Colorado.

Fig. 2. Photograph of Green Lake 4 taken from an aspect facing north in late August 1985.

tional descent between any pair of connecting lakes is 104 m between GL 4 and GL 3. Most of this vertical decline occurs via a steep waterfall near the outlet of GL 4, from the base of which the main stream and small tributaries follow a more gradual decline to GL 3 (Fig. 3). The linear distance between the inlet of GL 5 and the outlet of Lake Albion is 5 km.

Only GL 1 (3,426 m) is apart from the main flowage system. This lake has no inlet, but it has a subterranean seepage that surfaces as a small stream (Stream 1), ultimately draining into Lake Albion. GL 1 (Fig. 4) has an open, south-facing exposure with a steep talus slope to the north and less-steep rises to the east and west.

The maximum depths of the lakes are 8 m for GLs 1 and 5, 13 m for GL 4, 16 m for GLs 3 and 2, and 14 m for Lake Albion. The bottom composition of most littoral zones of lakes, and of streams, is a mixture variously dominated by one or more of the following: boulders, large to small stones, and sometimes patchy areas of coarse to fine sand and silt. The bottom of the central and deeper portions of the lakes is almost entirely silt-clay (McNeely 1983). The lower lakes had a longer ice-free season in all years. Lake Albion and GL 1 reached maximal temperatures of 13 and 14 C, respectively, in August and early September of 1981 and 1982. Lakes 4 and 5 never experienced maxima much above 9 C. Data published by Caine (1984) indicate that pH values of the flowage water were nearly always between 6 and 7.

Fig. 3. Photograph of Green Lake 3 taken from an aspect facing west. Waterfall in background is part of Stream 4 below outlet from Lake 4, August 1985.

Fig. 4. Photograph of Green Lake 1 taken from an aspect facing north in early October 1986. Green Lake 1 is the only lake separated from the main drainage and with a full southern exposure.

Lake Albion, GL 2, and GL 3 support populations of brook trout (*Salvelinus fontinalis*) (Nelson 1976, Windell, unpublished data). Green Lakes 1, 2, 3, and Lake Albion have been enhanced in volume by the construction of dams. Repair of these dams during the summer of 1985 necessitated a lowering of water levels by opening conduits near the bottom of lake basins. Water levels returned to normal in 1986 except in GL 2 where barrier damage was greatest.

METHODS

Benthic macroinvertebrates were collected between 1 July and 20 October 1981 at two-week (sometimes three-week) intervals, with later beginning dates in succeeding years. Specimens were collected from three predetermined and regularly sampled lake sites (except GL 2) and at intervening stream sites.

The benthos was sampled using a rock-picking technique in the lakes and the Surber-sampling method in the intervening streams. The rock-picking involved turning over randomly selected rocks within the range of the sampling site. Organisms on the rocks (sometimes on finer bottom sediments) were then removed with fine forceps. All picking times were standardized to 15 minutes. In addition to rock-picking, vegetation samples were taken from several lakes and streams. As all of the lakes have a generally narrow littoral zone, rock-picked (or bottom-picked) samples were most often obtained up to 3 m (infrequently as much as 6 m) from shore.

Surber-sampling stations in the streams generally were located either close to the outlet of one lake or the inlet of the succeeding lake, but the station between Green Lakes 3 and 2 was situated approximately equidistant from each lake. Two 1-min samples were taken 1–3 m apart at each station. Because of their proximity, these two samples were combined to give numbers of organisms per 0.09 m^2. The net mesh was 1024 um. When samples were unusually dense or confounded with excessive amounts of entangling vegetation, aliquots were taken. The sample was first poured into an enameled pan and agitated either manually or with a magnetic stirrer. Then an aliquot, the volume of which was determined by the nature of the sample, was taken. A total of three aliquots was used from each sample. Specimens were preserved in 70% ethanol prepared with 5% glycerine. If field samples were placed in 5% formalin, they were later changed to the alcohol-glycerine solution.

TAXONOMIC IDENTIFICATION

Identification of aquatic insects was done by us almost exclusively from the immature aquatic stages, with samples confirmed by the taxonomic specialists cited below in the Acknowledgments. A large body of literature was used for identification (Allen and Edmunds 1962, Arnett 1960, Baumann et al. 1977, Beck 1976, Bode 1983, Brinkhurst and Cook 1966, Brinkhurst and Jamieson 1971, Dodson 1982, Edmunds et al. 1976, Elgmork and Saether 1970, Fiance 1977, Harmston 1963, Hiltunen and Klemm 1980, Klemm 1982, Lepneva 1966, Mason 1973, Merritt and Cummins 1984, Morihara and McCafferty 1979, Oliver et al. 1978, Pennak 1978, Peterson 1970, Roback 1957, Saether 1970, 1975, 1976, 1977, Simpson and Bode 1980, Smith 1968, Soponis 1977, Steyskal and Knutson 1981, Stone 1981, Surdick 1981, Szczytko and Stewart 1979, Usinger 1956, Ward 1985, Wiggins 1977, Wilson and McGill 1982, Wu 1978).

RESULTS

The 1981 and 1982 collecting seasons (July–October) of the current study produced a total of 111 taxa, 93 of which occurred in streams (Table 1). Stream samples obtained by Elgmork and Saether (1970) in the first two weeks of July 1960 included 71 taxa of benthic macroinvertebrates. Of the 111 taxa included in our study, 64 were exclusively lotic, 18 were restricted to lentic sites, and 29 were both lentic and lotic in occurrence. At any particular collecting site the Chironomidae accounted for 31–51% of taxa in streams and 22–67% in lakes during 1981. Many taxa (30%) of the Green Lakes Valley flowage system were represented by a single specimen. About half of these were dipterans, thus underscoring the contribution of these insects to community diversity.

Species richness in the littoral-benthic zone of these lakes ranged from 9 to 19 taxa. Dredge samples from deeper water presumably would raise these values by contributing additional chironomids, oligochaetes, and nematodes. Mean Shannon-Weiner species diversity was 2.15 ± 1.08 for all lakes sampled in 1981 and 1982. In lotic habitats, species richness ranged from 24 to 40 taxa, and mean species diversity was 2.33 ± 0.75. Species diversities of Green Lake 1 and Stream 1 were both higher than mean diversities of all lakes and streams. While community composition changed with elevation, there was no trend in actual species number.

DISCUSSION

NUMERICAL ABUNDANCE AMONG SUPRA-GENERIC TAXA.—Distribution of organisms among major taxonomic groups remained comparatively stable over the 21-year period between the 1960 collections and the present study. The benthos of streams and lakes of Green Lakes Valley was predominantly dipterans. The Diptera constituted 81% of total macroinvertebrate organisms in streams in 1960, and 79% and 73% in 1981 and 1982, respectively. Worms (Nematoda, Oligochaeta, Turbellaria, and Hirudinea), Ephemeroptera, Plecoptera, Trichoptera, and other taxa (Coleoptera, Mollusca, and Crustacea) individually accounted for less than 10% of total abundance in 1960, 1981, and 1982, with the exception of worms in 1982, which constituted 15% of lake and stream abundance.

A similar preponderance of dipterans became evident when abundances of organisms for streams alone were compared. However, lake organisms were predominantly trichopterans (44–60% of total abundance) and dipterans (24–39%). Worms, Ephemeroptera, Plecoptera, and other organisms independently constituted less than 10% of organisms collected in both 1981 and 1982. Again, deep-water dredge samples from lakes would likely increase the proportions of the dipterans, oligochaetes, and nematodes. Therefore, the somewhat contrasting importance of dipterans in lakes and streams is explained, in

TABLE 1. Benthic organisms of lakes and streams in the Green Lakes Valley, Boulder County, Colorado, for 1960 and 1981–1982. (New occurrences for later years: *1983, **1984, ***1985).

Organism	Relative abundance		Location
	(1960)[1]	Present study	Present study
CNIDARIA			
Hydra sp.	less ab.	ab.	L(3,A), S(1)
PLATYHELMINTHES (Turbellaria)			
Polycelis coronata	ab.	ab.	L(A,3,4,5), S(1,2,3,5)
NEMATODA sp.	ab.	less ab.	L(A), S(1,5)
BRYOZOA			
Plumatella sp. statoblast	less ab.	—	—
Plumatella repens	—	rare	L(A)
Fredericella sultana	—	ab.***	L(3)
HIRUDINEA			
Glossiphonia complanata	—	rare	L(1)
OLIGOCHAETA			
Analycus sp.	—	ab.	L(3), S(1)
Chaetogaster cf. *Diastrophus*	ab.	—	—
Mesenchytraeus sp.	ab.	—	—
Nais variabilis	ab.	ab.	L(3), S(1,2,4,5)
Tubificidae sp.	—	rare	L(A), L(5)
Lumbriculus variegatus	—	less ab.	L(3)
AMPHIPODA			
Gammarus lacustris	less ab.	ab.	L(1), S(1)
ACARINA			
Atractides sp.	—	rare**	S(1)
Aturus fontinalis	ab.	—	—
Lebertia atelodon	less ab.	less ab.*	S(1)
Limnochaetes americana	—	rare	L(3)
Sperchon coloradensis	less ab.	less ab.	L(A), S(1)
COLLEMBOLA			
Podura aquatica	less ab.	rare	S(5)
EPHEMEROPTERA			
Siphlonuridae			
Ameletus sp.	—	ab.	L(3,4), S(4,5)
Siphlonurus sp.	—	rare	L(A), S(5)
Baetidae			
Baetis bicaudatus	ab.	ab.	S(1,2,3,4,5)
Baetis intermedius	less ab.	—	—
Baetis rusticans	less ab.	—	—
Baetis tricaudatus	—	ab.	S(5)
Heptageniidae			
Cinygmula mimus	ab.	ab.	L(3,4), S(1,3,4)
Ephemerellidae			
Drunella coloradensis	ab.	ab.	S(2,3)
PLECOPTERA			
Nemouridae			
Nemouridae sp.	—	less ab.	S(1,4,5)
Malenka sp.	—	rare	S(2)
Nemoura sp.	less ab.	—	—
Nemoura arctica	—	less ab.	S(5)
Zapada cinctipes	—	less ab.	S(1,2)
Zapada haysi	less ab.	—	—
Zapada oregonensis	—	less ab.	S(1)
Leuctridae			
Paraleuctra or *Perlomyia* sp.	—	less ab.	L(5)
Capniidae			
Bolshecapnia, *Capnia*, *Mesocapnia*, or *Utacapnia* sp.	—	less ab.	L(5)

Table 1 continued.

Organism	Relative abundance		Location
	(1960)[1]	Present study	Present study
Perlodidae			
Cultus sp.	—	ab.	S(1,3)
Isogenus sp.	ab.	—	—
Isoperla fusca	—	rare	S(2)
Isoperla quinquepunctata	—	less ab.	S(3)
Kogotus modestus	—	rare	S(3)
Megarcys signata	—	ab.	S(3)
Skwala parallela (?)	—	rare	L(4)
Sweltsa sp.	—	ab.	L(A), S(1,2,3,4)
HEMIPTERA			
Notonectidae			
Notonecta sp.	—	rare	L(1)
TRICHOPTERA			
Trichoptera spp., early instars	—	ab.	L(1,A), S(1)
Rhyacophilidae			
Rhyacophila sp.	ab.	—	—
Rhyacophila acropedes (e)	—	rare	S(1,5)
Rhyacophila angelita	—	less ab.***	S(2,3)
Rhyacophila hyalinata (e)	—	rare	L(3), S(2,3)
Rhyacophila tucula	—	less ab.	S(1,2,3,4,5)
Lepidostomatidae			
Apatania sp.	—	ab.	L(1,A), S(2)
Brachycentridae			
Brachycentrus sp.	ab.	—	—
Limnephilidae			
Hesperophylax sp.	ab.	—	—
Hesperophylax occidentalis	—	ab.	L(1–5), S(1–4)
Hesperophylax oreades (c)	ab.	—	—
Psychoglypha subborealis	—	less ab.	L(A,1)
Psychoronia costalis (c)	—	ab.	L(A,1,4,5), S(4)
Leptoceridae (adult)	—	rare	S(1)
LEPIDOPTERA			
Pyralidae sp.	—	rare	S(1)
COLEOPTERA			
Dytiscidae			
Agabus sp.	—	rare	L(1), S(5)
Dytiscus sp.	—	rare	S(1)
Hydrophilidae			
Helophorus sp.	—	less ab.	S(3)
Staphylinidae			
Staphylinidae sp.	—	rare	S(2)
Elmidae			
Heterolimnius corpulentus	—	rare	S(1)
Zaitzevia sp.	—	less ab.	S(1)
Heteroceridae			
Heterocerus sp.	—	rare	S(5)
Georhyssidae			
Georhyssus sp.	—	less ab.	S(4)
DIPTERA			
Sciaridae			
Sciaridae sp. A	less ab.	—	—
Sciaridae sp. B	less ab.	—	—
Lycoriella (Hemineurina) sp.	less ab.	—	—

Table 1 continued.

Organism	Relative abundance		Location
	(1960)[1]	Present study	Present study
Empididae			
Atalanta sp.	ab.	—	—
Clinocera (Hydromia) sp.	—	less ab.	S(2,4,5)
Tipulidae			
Antocha sp.	—	less ab.	S(3)
Dicranota sp.	—	ab.	S(1,2,3,4,5)
Erioptera (trimicra) sp.	—	less ab.	S(1)
Limnophora torreyae (e)	—	less ab.	L(1), S(5)
Ormosia sp.	—	less ab.	S(1)
Tipula sp.	—	less ab.	S(5)
Culicidae			
Culicidae sp.	—	rare	L(5)
Aedes spp.	—	less ab.	S(2)
Aedes (Ochlerotatus) impiger	less ab.	—	—
Simuliidae			
Metacnephia sp. near *jeanae*	—	dom.	S(4,5)
Prosimulium (Prosimulium) hirtipes	ab.	rare	S(4)
Prosimulium (Prosimulium) travisi	ab.	less ab.	S(4)
Prosimulium (Prosimulium) ursinum (d,4)	ab.	—	—
Prosimulium (Prosimulium) sp. near *frohnei*	—	ab.	S(4,5)
Prosimulium n. sp. (d)	—	ab.	S(4,5)
Simulium hunteri	—	ab.	L(A), S(1)
Ephydridae			
Philygria debilis	—	rare	S(4)
Cressionella montana	less ab.	—	—
Thaumaleidae			
Thaumaleidae sp.	—	less ab.*	L(3 or 4)
Thaumalea sp.	less ab.	—	—
Chironomidae			
Chironomidae spp., larval bodies	—	less ab.	L(4), S(2,4,5)
Chironomidae spp., pupae	—	less ab.	L(3,5,A), S(4,5)
Chironomus anthracinus group	less ab.	—	—
Cardiocladius sp.	ab.	less ab.	S(5)
Chaetocladius	—	less ab.	L(A)
Corynoneura sp.	less ab.	—	—
Corynoneura taris	—	less ab.	S(5)
Cricotopus sp. 9	—	less ab.	L(3)
Cricotopus sp. B	—	rare	L(3)
Diamesa sp. A (4)	ab.	—	—
Diamesa sp. B	ab.	—	—
Diamesa sp. C	ab.	less ab.	S(3,4)
Diamesa sp. D	ab.	—	—
Diamesa sp. E	less ab.	less ab.	S(4,5)
Diamesa sp. F	ab.	less ab.	S(2,4,5)
Diamesa sp. G	ab.	less ab.	S(3,4)
Diamesa (Pseudokiefferiella) sp. H(4)	ab.	—	—
Diamesa (Pseudokiefferiella) sp. J	less ab.	—	—
Diamesa latitarsis gr.	—	ab.	S(3,5)
Diplocladius sp.	—	less ab.	L(3)
Eukiefferiella sp. A	less ab.	—	—
Eukiefferiella sp. (subtype bavarica) sp. B (a,4)	ab.	—	—
Eukiefferiella sp. C	less ab.	—	—
Eukiefferiella sp. D	less ab.	—	—
Eukiefferiella (type longicalcar) sp. E (b)	ab.	—	—
Eukiefferiella sp. F	less ab.	—	—
Eukiefferiella (subtype minor) sp. G (b)	ab.	—	—
Eukiefferiella sp. H	less ab.	—	—

Table 1 continued.

Organism	Relative abundance		Location
	(1960)[1]	Present study	Present study
Eukiefferiella coerulescens group	—	ab.	L(3), S(4,5)
Eukiefferiella devonica group	—	rare	S(2)
Eukiefferiella gracei group, sp. 1 (b)	—	ab.	S(4,5)
Eukiefferiella gracei group, sp. 2 (b)	—	less ab.	S(1,3,4)
Eukiefferiella rectangularis group, Type J	ab.	dom.	S(1,2,4,5)
Glyptotendipes (Phytotendipes) lobiferus (?)	—	ab.	L(1), S(1)
Heptagyia sp.	ab.	—	—
Heterotrissocladius hirtapex	—	rare	S(1)
Hydrobaenus fusistylus	—	dom.	L(3), S(4,5)
Metriocnemus sp. A	less ab.	—	—
Metriocnemus sp. B cf. *Epoiicladius* sp.	less ab.	—	—
Microcricotopus sp. *parvulus* type	less ab.	—	—
Micropsectra sp.	ab.	—	—
Micropsectra sp. 1	—	dom.	L(3,A), S(1,3,4,5)
Micropsectra sp. 2	—	rare	L(5)
Nanocladius (Nanocladius) spiniplenus	—	rare	S(2)
Orthocladiinae spp.	—	less ab.	L(A), S(5)
Orthocladius sp.	—	rare	S(2)
Orthocladius (Eudactylocladius) sp. A	less ab.	less ab.	S(4)
Orthocladius (Eudactylocladius) sp. B	ab.	ab.	L(3), S(1,2,4,5)
Orthocladius (Euorthocladius) sp.	ab.	—	—
Orthocladius (Euorthocladius) type III	—	ab.	L(3,4), S(1,3,4,5)
Orthocladius (Orthocladius) obumbratus	—	rare	S(2)
Pagastia sp. 1	—	less ab.	S(2,3,5)
Parakiefferiella sp.	ab.	rare	S(1)
Parametriocnemus graminicola	—	less ab.	S(2,3)
Paraphaenocladius sp.	less ab.	—	—
Phaenopsectra sp.	—	less ab.	L(3,5), S(5)
Procladius sp.	—	less ab.	S(1)
Psectrocladius sp.	—	less ab.	L(3,A)
Psectrocladius octomaculatus	less ab.	—	—
Pseudodiamesa pertinax	ab.	ab.	L(4,A), S(5)
Rheocricotopus sp. *atripes* type	less ab.	—	—
Rheocricotopus sp. *effusus* type	less ab.	less ab.	S(2)
Synorthocladius sp.	—	ab.	L(3), S(4,5)
Theinemannia cf. *gracilis*	less ab.	—	—
Trichotanypus sp.	—	rare*	L(5)
Tvetania bavarica group (a)	—	ab.	L(3), S(1)
MOLLUSCA			
Sphaeriidae			
Pisidium sp.	less ab.	—	—
Pisidium casertanum	—	ab.	S(1,4)
Pisidium nitidum	—	rare	S(1,4)
Pisidium variable	—	rare	S(1)

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[1] Elgmork and Saether (1970) Collections from 1960: ab. = 38 most abundant taxa based upon individuals sampled per 10-minute interval. less ab. = all other taxa.

[2] Present study. rare = 1, less ab. = 2–19, ab. = 20–299; dom. = >300 organisms collected during field season.

[3] Distribution data are given for present study only: S = stream (1,2,3,4,5). L = lake (A,1,2,3,4,5). See Fig. 1.

[4] Found by Elgmork and Saether (1970) outside of present study area.

[a] *Eukiefferiella* (subtype bavarica) sp. B (Elgmork and Saether 1970) is equivalent to *Tvetania bavarica* group in present study (Peterson 1983, personal communication).

[b] *Eukiefferiella* (subtype minor) (type longicalcar) sp. E + G (Elgmork and Saether 1970) are equivalent to *E. gracei* group in present study (Peterson 1985, personal communication).

[c] *Hesperophylax oreades* (Elgmork and Saether 1970) is equivalent to *Psychoronia costalis* in present study (Wiggins 1983, personal communication).

[d] *Prosimulium (Prosimulium) ursinum* (1970) is equivalent to *Prosimulium* n. sp. in present study (Peterson 1983, personal communication).

[e] Species designation tentative.

part, by the restriction of lake sampling to the narrow littoral zone.

NUMERICAL ABUNDANCE AMONG SPECIES.—The most abundant organism in 1981, the simuliid, *Metacnephia* sp. near *jeanae*, comprised 35.5% of all organisms collected. The absence of *Metacnephia* in 1960 may be due to the early sampling time in that year. Peak abundance in 1981 and 1982 was in late July and again in early September. In 1985 it was during August.

The most abundant stream species in 1960, the chironomid *Eukiefferiella* sp. G, may have been present in 1981 and 1982 as *E. gracei* species 1 and 2. A new taxon, *E. rectangularis*, a species first found in 1981, was fourth in abundance and was distributed throughout the same range of streams as was *Eukiefferiella* sp. G 21 years earlier. Perhaps these latter two organisms are temporally separated conspecifics.

Simuliids generally were dominants in 1960, 1981–1982, and 1985. *Prosimulium hirtipes* and *P. travisi* together formed the second most abundant group in 1960. Their dominance was replaced in 1981–1982 by *Prosimulium (Prosimulium)* near *frohnei* and *Prosimulium* n. sp. B., both of which were abundant. *Prosimulium* was concentrated in both studies in Streams 4 and 5, and also below Lake Albion in 1960 (outside the present study area). The recent manipulations of water levels in the lower lakes appear to have greatly reduced *Prosimulium* in Streams 3, 2, and 1.

Subdominants in 1960 included the chironomid *Diamesa* sp. A. in streams above Lake 5 (outside present study area), oligochaete *Mesenchytraeus* sp. extending down into Stream 5, the chironomid *Cardiocladius* sp., and *Eukiefferiella* sp. J., ranging throughout Streams 4 and 5. In 1981, subdominants were chironomids *Hydrobaenus fusistylus* in lentic and lotic situations above Stream 3; *Micropsectra* sp. 1, distributed throughout the study area; and the bivalve *Pisidium casertanum*, restricted to Streams 1 and 4 (GL 3, 1985).

Elevational distribution.—Elevational trends were apparent for several major taxonomic groups in lakes, but not in streams. Ephemeroptera and Trichoptera were more abundant in upper lakes (GLs 5 and 4) than in lower ones (Lake Albion and GL 1). These groups consisted mainly of shredders and scrapers. Dipterans were most abundant in lower lakes where rocks in the littoral zone were more often coated with a thin film of fine sediment and micro-Aufwuchs.

Several taxa showed elevational range affinities in both 1981 and 1982. The blackfly *Metacnephia* (a filter-feeder) was especially numerous in Stream 5 (just below the GL 5 outlet) and extended in small numbers down to Stream 3. It is possible that GL 5 serves as a catchment for coarse and fine particulate organic matter derived from extensive *Kobresia*-alpine avens wetlands in the surrounding alpine basin. Studies of suspended particulate organic matter in the waters of Green Lakes Valley are not yet completed but possibly will have a bearing on this contention. Little is known about the physiology or aerodynamic suitability of the adults of this genus that may contribute to its successful breeding in this harsh environment.

Baetis bicaudatus (an ephemeropteran collector-gatherer) and *Hesperophylax* (a trichopteran shredder) were distributed throughout the watershed in both years, but they were particularly abundant during the summer of 1982 in Stream 5. This may be attributable to an especially long growing season on the high tundra in 1981, resulting in large allochthonous detrital food reserves in the stream the following year.

Ephemeropterans are microhabitat specialists sensitive to subtle differences in stream substrates and water velocities (Edmunds et al. 1976). The abundance of *Cinygmula mimus* (a scraper) in Stream 4, *Drunella coloradensis* (an engulfer and scraper) in Stream 3, and *Ameletus* (a scraper) in upper streams and lakes (i.e., Ss 5 and 4, GLs 5 and 4) may be the result of such microhabitat partitioning. *Ameletus* and *Cinygmula* are genera with usually lotic species, but they are found in lentic habitats in Green Lakes Valley. However, hydrological studies indicate that these lakes are constantly flushing systems and have currents in some locations throughout the summer months (Caine 1984).

Uniqueness of Lake 1, Stream 1.—Green Lake 1 and its outlet, Stream 1, are isolated from the main flowage of North Boulder Creek and have certain unique characteristics. Tributaries of this spur on the main drainage carry higher solute loads than other tributaries in the valley (Hoffman et al. 1985). Green Lake 1 is also the only lower lake in the valley without a fish population. The amphipod *Gammarus lacustris* and the leech *Glossiphonia complanata* were restricted to this lake and stream. A longer ice-free season because of shallowness and full southern exposure, higher solute values, and a lack of fish predators may contribute to the success of these species here. During a draw-down of GL 1 in the summer of 1985, *G. lacustris* mortality was very high (estimates average 2/cm^3) in evaporation pools at the receding lake edge. This species may well be the greatest producer of animal biomass in GL 1.

Three species of fingernail clams (Sphaeriidae: *Pisidium casertanum*, *P. nitidum*, and *P. variabilis*) are sympatric in Stream 1. *Pisidium casertanum* was the fifth most abundant organism in the 1981 field season, abundant in Stream 1, and less so in Stream 4 (three dried specimens were found on the lake bottom of GL 3 in 1985 after the lowering of the water level). *Pisidium variabilis* was represented by only one specimen collected in Stream 1. The geographical distribution of most freshwater bivalves is limited by water chemistry, as more alkaline water with elevated calcium carbonate favors larger numbers of individuals and species. However, Sphaeriidae construct shells in remarkably low concentrations of calcium carbonate (Pennak 1978). It is not uncommon to find *Pisidium* in alpine waters with very low dissolved solute concentrations, but its abundance in Stream 1 in 1981 and 1982 may reflect higher solute concentrations in this region of the Green Lakes Valley, consonant with a more efficient detrital trap (dictated by slow seepage into Stream 1 from GL 1). The three clam species can coexist in habitats only as low as pH 5.5–6.0 (Okland 1980, Okland and Kuiper 1980), which overlaps the lowest reading for Green Lakes flowage.

In 1985 there was a notable decline of the *Pisidium* population in Stream 1. The lowered water level in GL 1 reduced the flow in Stream 1 to a trickle. This stressful condition and a pH near the known lower tolerance level for *Pisidium* species are probably important factors contributing to the decline.

BRYOZOA.—Only a single statoblast of an unidentified species of *Plumatella* was found by Elgmork and Saether (1970). A colony of *Plumatella repens* with only five zooids was obtained from Lake Albion in 1982. However, the surprise during the 1985 season was the preponderance of *Fredericella sultana* on the rocks in Green Lake 3. The water level in this lake was lowered approximately 6.4 m for dam repair. This change in water level exposed a considerable, normally submerged, rocky benthic area. Inspection of several rocks found to have dry colonies of *F. sultana* suggested that we should take radial transects (from the former lake margin to the lowered water line). Easily dislodged small- to medium-sized rocks along seven transects were examined. Forty-three percent (91 of 212 rocks) had one or more dried *F. sultana* colonies attached. Many of these colonies were large, i.e., > 75–100 zooids, a few up to several hundred. Subsequently, numerous luxuriant living colonies were observed on submerged rocks at the water line and deeper down. Large colonies grow away from a surface as easily seen, loose tufts. *Fredericella sultana* has been reported from high-elevation Swiss lakes by Forel (1884). Bushnell (1966) found this species surviving and slowly growing under lake ice all winter in Michigan. In GL 3 no colonies were found above the 1.3-m depth; thus, the species was below the level of the winter ice thickness. Since this species does not produce floating statoblasts, the primary means of settling on near-surface substrates is via the sexually produced larvae. If colonies had been seasonally established on such substrates in GL 3, freezing and ice abrasion likely obliterated them.

The most striking aspect of the Green Lake 3 fauna is that the largely rocky benthic regions, to as far down as we have observed, are dominated by a bryozoan macroinvertebrate. Such dominance is not commonly encountered in warmer eutrophic lakes and was heretofore unknown for a truly alpine or arctic lake.

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DISTRIBUTION OF VERTEBRATES OF THE BIGHORN CANYON NATIONAL RECREATION AREA

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ABSTRACT.—During a survey of the vertebrates in the Bighorn Canyon National Recreation Area, 46 mammal, 210 bird, 9 reptile, 5 amphibian, and 28 fish species were found. Habitat structure and moisture were two environmental variables associated with species numbers across this 1,820-ha area. Eight distinct habitats were evaluated. In coniferous forests, 27% of the birds and 54% of the mammals were observed. Sagebrush/grasslands and upland shrublands were very arid and had relatively few vertebrates. Five introduced game birds occurred in sagebrush habitat. Riparian and wetland habitats had the largest number of unique vertebrates, 38 and 77 respectively. The establishment of Bighorn Lake in 1968 influenced the fisheries in streams and rivers as 10 introduced fish species are now there.

The Bighorn Canyon National Recreation Area (BCNRA) in north central Wyoming and south central Montana provides an array of habitats. Climate and rain shadows have a major impact, resulting in arid, high prairie being the dominant habitat. However, varied habitat types provide homes for many species of fish and wildlife. While moisture has a major influence on habitat and thus fish and wildlife, people have also impacted heavily on the region. Direct forms of habitat alteration through grazing, brush removal, and fire suppression have changed species composition. Perhaps more dramatic changes have resulted from introduction of exotic species.

The objectives of our study were: (1) to determine patterns of vertebrate species richness within BCNRA, (2) to determine habitat features influencing species distribution and species richness patterns, and (3) to examine the influence of people on vertebrate distribution and species richness.

STUDY AREA

The BCNRA lies between the Bighorn Mountains to the east and the Pryor Mountains to the west. Elevation ranges from 1,120 m above sea level near Fort Smith, Montana, to 2,355 m in the Pryor Mountains, Wyoming. The BCNRA is approximately 12 km northeast of Lovell, Wyoming, and 40 km southeast of Billings, Montana. Habitat types are highly diverse in the area that extends 90 km from north to south. The north and south ends are wide, flat valleys, while the central portion is a rolling plain cut by the 335-m-deep Bighorn Canyon.

There is wide seasonal and geographic variation in temperature and precipitation. Annual temperatures range from −26 C to over 38 C ($\bar{x} = 10$ C). A precipitation gradient exists between Lovell, a desert with only 18 cm of precipitation/year, and Fort Smith, a grassland with over 50 cm of precipitation/year (National Park Service 1981).

In the south, plant communities consist primarily of saltbush (*Atriplex* spp.) and greasewood (*Sarcobatus* spp.) in drier sites, while along the Bighorn River, Shoshone River, and the Bighorn Lake, plains cottonwood (*Populus deltoides*) is found. Further north, communities of Utah juniper (*Juniperus osteosperma*), sagebrush (*Artemisia* spp.), mountain mahogany (*Cercocarpus ledifolius*), and grasslands dominate the uplands. Several small creeks flow eastward from the Pryor Mountains, and in these riparian areas narrowleaf cottonwood (*Populus augustifolia*), skunkbush (*Rhus trilobata*), and other woody vegetation are found. A Douglas-fir (*Pseudotsuga menziesii*) forest covers most of the upper portions of the Pryor Mountains, with limber pine (*Pinus flexilis*) occurring on the lower benches. North of the Pryor Mountains near Dry Creek, stands of ponderosa pine (*Pinus ponderosa*) and Douglas-fir occur on most north-facing slopes; mountain mahogany is common on the south-facing slopes. The riparian zones in this area consist mainly of boxelder (*Acer negundo*), chokecherry (*Prunus virginiana*), water birch (*Betula occidentalis*), and other species of shrubs and trees. Small stands of ponderosa pine are found near Fort Smith, and grasslands in the vicinity are indicative of a mixed prairie.

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In 1968 the Yellowtail Dam was completed near Fort Smith, Montana. The dam formed the 113-km-long Bighorn Lake on the Bighorn River within Bighorn Canyon. Some maps incorrectly refer to the Bighorn Lake as the Yellowtail Reservoir. Normal pool elevation is 1,213 m, but much variation occurs (National Park Service 1981). Causes of this variation are complex but include weather, depth of mountain snowpack, flow-rate adjustments made at Boysen and Yellowtail dams, and evaporation rates. Changes in the surface area of the reservoir are minor at the north end because of steep canyon walls, but at the south end the reservoir inundates large, shallow areas along the Bighorn and Shoshone rivers (National Park Service 1981). When the pool level is low, these floodplains are dry, greatly reducing the amount of wetlands present.

Additional aquatic environments consist of the two headwater rivers and several small streams. The Bighorn and Shoshone rivers are relatively warm, silt-laden rivers upstream from Bighorn Lake. Seventeen streams flow into Bighorn Canyon. These are mostly small streams, many ephemeral, that have downcut channels in steep, narrow canyons. A few perennial, coldwater streams capable of supporting salmonids are found in the area.

While the addition of Bighorn Lake is a recent impact to the Bighorn Basin, this land has been impacted by people for more than 10,000 years. Early Indian hunters sought food there. Later Crow Indians settled around the Bighorn Canyon. Explorers and trappers came in the early nineteenth century. Trails were established across the area to reach mines in Montana around the time of the Civil War. Large cattle ranches were established some 15 years following the war. Today land-use practices within and adjacent to the BCNRA include grazing, farming, mining, and recreational activities.

METHODS

Two seasons of field investigations were conducted on BCNRA. During 1984 data were collected on birds and mammals. In 1985 field data collection emphasized fish, amphibians, and reptiles.

Birds were observed while walking transects. The use of binoculars and a spotting scope helped establish at least two transects of 300–1,000 m in each vegetation type. Birds seen or heard within 15 m of the transect were recorded. Transects were walked at least five times.

Mammals were surveyed by incidental observations of species and tracks. Small mammals were captured by setting 20 museum specials, 5 rat, and 10 pit traps along transects in each habitat. Two snap traps and one pit trap were set at 10-m intervals along transects, although pit and snap traps were not set simultaneously. Bats were captured in two mist nets set near or over wetlands, at heights of 2.5–5.0 m and 1.5–3.0 m. Each net was 20 m long and 2.5 m wide. Voucher specimens were deposited in the vertebrate museum at the University of Wyoming.

Electrofishing was done 20–23 June 1985 in the 12 largest perennial streams in the BCNRA: Black Canyon Creek, Little Bull Elk Creek, Big Bull Elk Creek, Hoodoo Creek, Dryhead Creek, Deadman Creek, Gypsum Creek, Trail Creek (north and south forks), Layout Creek, Porcupine Creek, and Crooked Creek. In most streams, electrofishing began at the mouth of the creek and continued upstream until fish were no longer captured or the BCNRA boundary was reached.

The Bighorn River was sampled using a 5-m-long, 5-mm mesh bag seine. Minnow traps were set in pools and under overhanging boulders in streams and on the bottom and within vegetative cover of emergent wetlands. Additional information on fish distribution was obtained from examining data collected by the Wyoming Game and Fish Department and the Montana Department of Fish, Wildlife, and Parks.

Herpetological searches were concentrated in wetlands and riparian areas in May, June, and early July to coincide with breeding seasons. Searches for snake dens were made in late August and September along south-facing ridges (Duvall et al. 1985) near Sykes Moun-

TABLE 1. Habitat types of Bighorn Canyon National Recreation Area. Modified from Cowardin et al. (1979) and Oakleaf et al. (1981).

1. Coniferous forest including Douglas-fir, limber pine, and ponderosa pine.
2. Upland shrub including juniper, mountain mahogany, sagebrush, greasewood, and rabbitbrush.
3. Sagebrush grassland.
4. Riparian including plains and lanceleaf cottonwood, boxelder, waterbirch, willow, chokecherry, and Russian olive.
5. Wetland including sedges, rushes, and cattail.
6. Streams.
7. Headwater rivers.
8. Reservoir.

tain and East Pryor Mountain. Specific habitat types were searched on foot, and straight-line transects were walked.

Three passive capture methods were used. Baited hoop nets were set in the Bighorn River for turtles. Baited minnow traps were set in wetland and riverine habitats for amphibians and small turtles. A combination of plastic mesh drift-fencing and 20-liter pitfall traps was used for snakes and lizards. Lizards were also noosed in areas where thick vegetation prevented hand capture. Road cruising on both paved and unpaved roads was used for sampling snakes (Campbell and Christman 1982).

RESULTS

The BCNRA study sites consisted of 1,820.8 ha of terrestrial and aquatic habitat plus Bighorn Lake. Eight distinct habitats were evaluated (Table 1). Sagebrush/grassland areas consisting of 698.8 ha (38.8% of the terrestrial habitat) were the most arid and often had rock outcrops. Upland shrub communities of juniper and mountain mahogany were also arid and consisted of 728.2 ha (40%). Mixed conifer forests were on 108.8 ha or 6%. Douglas-fir, rocky mountain juniper, ponderosa, and limber pine were the dominant tree species in these relatively dry forests. Riparian habitat included creek woodland and floodplain forests with narrowleaf cottonwood, Russian olive, box elder, elm (*Ulmus pumila*), Saskatoon serviceberry (*Amerlanchier alnifolia*), chokecherry, hawthorne (*Crataegus* sp.), wild rose (*Rosa* sp.), and mountain maple (*Acer glabrum*). Riparian areas made up 263.2 ha (14.4%) of the terrestrial habitat.

Wetlands were found on 21.8 ha (1.2%). Some wetland areas were mudflats. In the summer, emergent wetlands were created as water inundated the vegetation, which consisted of sedges (*Cyperus* spp., *Juncus* spp.), rushes (*Scirpus* spp.), and cattail (*Typha latifolia*).

Streams flowing into Bighorn Lake within BCNRA range from ephemeral watercourses to perennial, coldwater streams. Several are impacted by upstream uses such as water diversion and cattle grazing. The two headwater rivers, Bighorn and Shoshone, are relatively warmwater, turbid streams.

Water quality and discharge of these rivers are both strongly influenced by upstream water development and agricultural practices. Within BCNRA these two streams support a variety of warmwater fishes.

Bighorn Lake has impounded the Bighorn River within BCNRA. The reservoir is generally confined by the wall of Bighorn Canyon. It is deep with very little littoral area. At the headwaters there are expanses of shallow mud flats periodically exposed when the reservoir is drawn down. The reservoir supports a coldwater fishery with a variety of sport, forage, and rough fishes. Water quality changes over the length of the reservoir with eutrophic conditions near the headwaters and relatively oligotrophic conditions near the dam.

Species/Habitat Association

During the two-year project, 28 fish, 5 amphibians, 9 reptiles, 210 birds, and 46 mammals were found in BCNRA (Appendix). The number of vertebrate species found in each of the eight classes of habitat is listed in Table 2.

SAGEBRUSH AND GRASSLANDS.—Of the 98 species found here, 15 were unique in this habitat (Table 2). Say's phoebe and grasshopper sparrows were observed in the sagebrush flats near Crooked Creek. Brewer's sparrows were common in the sagebrush habitat on the dryhead range.

The only specimen of a northern grasshopper mouse was collected in the sagebrush flats near Crooked Creek. Ord's kangaroo rats were common there. One rare Merriam's shrew was captured in the sagebrush on the dryhead range, and tracks of black bears were found.

Table 2. Numbers of vertebrate species found in eight habitat types of BCNRA. Numbers in parentheses indicate number of species found only in that habitat. Habitats are shown in order from xeric to mesic.

Xeric —————————————————— Mesic

Habitats

Taxa	Sagebrush grassland	Upland shrub	Conifer forest	Riparian	Wetland	Streams	Headwater rivers	Reservoir	Total
[Code*]	1	2	3	4	5	6	7	8	
Fish					8(1)	19(1)	25(6)	28	
Amphibians	1(1)		1	4	4				5
Reptiles	5	5	5	4(1)	3(1)				9
Birds	61(11)	32(2)	58(10)	98(38)	98(74)				210
Mammals	31(3)	22	25	32(2)	15				46
Species totals	99(15)	59(2)	88(10)	156(38)	120(77)	9(1)	20(1)	25(6)	
Total hectares	698.8	728.2	108.8	263.2	21.8				1820.8
Proportion of area	38.8	40	6	14.4	1.2				100

*From Table 1

This was the habitat of the spadefoot toad, although it is not common in BCNRA. Horned and sagebrush lizards were found in these habitats. Bullsnakes, yellow-bellied racers, and milksnakes were observed in sagebrush habitat.

Upland shrub.—Few bird species nested in upland shrub habitats, and relative abundance of species appeared to be low. Mixed species flocks of birds were commonly seen moving through upland shrub habitats in the late summer and fall. Pocket mice were captured in a sagebrush-juniper area. An Ord's kangaroo rat was trapped in sandy soil in juniper and mountain mahogany. No amphibians were found in these dry habitats. The eastern short-horned and northern sagebrush lizard were observed here, as were the bullsnake, racer, and prairie rattlesnake.

Conifer forest.—Conifer forests had a variety of birds and mammals. Eleven species were found only in this habitat. In the more open forests of ponderosa and limber pine, Cooper's hawks and some flycatchers were observed. Associated with the understory vegetation were both green-tailed and rufous-sided towhees. Tiger salamanders were occasionally found on the forest floor.

Vagrans shrews and montane voles were captured in the ponderosa pine and Douglas-fir forests, where tracks of mule deer and elk also were frequently found.

Riparian.—Shrub and creek woodlands as well as floodplain cottonwood constituted riparian habitats of the BCNRA. These areas had a large number of species, considering their relatively small total area (14.4%). The riparian habitats had a comparatively high number of species (38) found only in that habitat. Many of the unique vertebrates there were birds. Eastern kingbirds, lazuli buntings, rufous-sided towhees, and lark sparrows nested there, while Brewer's blackbirds and green-tailed towhees were observed once during spring migration. Many birds observed there were also found in plains cottonwood forests.

Few species of mammals were trapped in these habitats, although one of two specimens of western harvest mice and the only western jumping mouse were captured in the mature stand of cottonwoods. A long-tailed weasel was seen, and white-tailed deer were common. Tiger salamanders, chorus frogs, and leopard frogs were found in creek woodlands and floodplain forests. These areas provided moisture necessary to sustain the amphibians. Creek woodlands had a number of the reptile species including the bullsnake, milksnake, gartersnake, and prairie rattlesnake.

Wetlands.—Most nesting bird species were associated with palustrine wetlands that had either emergent vegetation or mud shores. Dabbling ducks were observed using wetlands as brood habitat. Both pied-billed grebes and American coots nested in emergent wetlands. Emergent vegetation was commonly used by yellow-headed and red-winged blackbirds, marsh wrens, and common yellowthroats. MacGillivray's warblers and song sparrows were common in the shrub willow near shore. Because of the many aquatic and water birds found in wetlands, these areas had the highest (77) number of unique species.

Mammals trapped in the wetlands were

mostly deer mice, although a western harvest mouse was collected in a stand of cattails. Mink were observed in an emergent wetland south of the causeway. Chorus and leopard frogs, woodhouse's toad, and tiger salamanders were found in wetlands with several snakes and painted turtles.

Streams.—Five species of fish were captured by electrofishing in streams (Appendix). Fish were found in only 6 of 12 perennial streams: Black Canyon Creek, Big Bull Elk Creek, Dry Head Creek, Deadman Creek, Gypsum Creek, and Porcupine Creek. Only the four largest streams contained salmonids. Most fish were captured in riffles or in pools beneath overhanging boulders.

Headwater rivers.—The fish species known to occur in the headwater rivers were quite varied and included at least 19 species. Many species were ephemeral residents of rivers, using them during the spawning seasons. A variety of nongame fishes resided in the headwater rivers during much of the year. They included the lake chub, sturgeon chub, flathead chub, longnose dace, river carpsucker, longnose sucker, white sucker, shorthead redhorse, and stonecat. The headwater rivers had low sport fishing value within BCNRA.

Reservoir.—The reservoir in both Montana and Wyoming supported a substantial sport fishery. Sport fish introductions into the reservoir have lead to at least 10 additional fish species. While centrarchids have been introduced, they were not a dominant family because of the limited littoral areas, relatively cold water, and fluctuations in water levels. The reservoir had the greatest diversity of fish species (25) as a result of the diversity of habitat features encountered over its length. Six fish were found only in the reservoir. Twenty-seven species occurred in the reservoir or rivers entering the reservoir as observed by the Wyoming Game and Fish Department and the Montana Department of Fish, Wildlife and Parks, which routinely surveyed these waters (Appendix).

Shifts in Species Richness

Each habitat type provided features that attracted species. Both habitat structure and moisture, which are examined in the discussion, influenced species richness. The drier habitats had fewer species than the terrestrial moist habitats (Table 2). Structure, however, influenced the total species count. Conifer forests, for example, had more birds than did the sagebrush/grassland and upland shrub habitats. No amphibians or reptiles were found in forest communities. Birds were in much higher numbers in riparian and wetland habitats. Thus, the changes in total species numbers were seen more in birds than in any of the other vertebrate groups.

Introduced Species

As people have come to BCNRA, vertebrate species have been introduced into the region. No introduced amphibians, reptiles, or mammals were found, although wild horses were in the region at one time. Introduced birds were primarily game birds: ring-necked pheasant, chukar, grey partridge, and turkey. These species were in sagebrush grassland, with the turkey also using forest and riparian habitats. Starlings were common in wetlands, and house sparrows were common around buildings and bridges.

Of the 28 species of fish known to occur in BCNRA, 10 have been introduced by fishery managers for the purpose of enhancing sport fish diversity. Several species have been stocked in the reservoir since its construction: rainbow trout, brown trout, lake trout, largemouth bass, green sunfish, black crappie, white crappie, and yellow perch. Additional species introduced in the nineteenth century include the brook trout and common carp.

Discussion

The results of our study on BCNRA indicated the importance of two habitat features, moisture and structure. Moisture seemed to have an even more pronounced influence on vertebrate species in the arid region. Combining the riparian and wetland terrestrial habitat, we accounted for only 15.6% of the area. These areas, however, had the more diverse population of vertebrates of the BCNRA. Many of the migratory birds were observed there. Shorebirds and waterbirds, as well as colonial nesting birds, were only in marsh habitat. Creek woodlands, which accounted for only 0.5% of the area, had 30% of the nesting birds. The moist habitat contained 11 of the 46 species of mammals and 9 of the 19 reptiles and amphibians.

Others have shown the importance of moist habitats for vertebrate species. In southern Wyoming, Krueger and Anderson (1985) found that birds utilized shrub willow communities in higher proportion than other habitats. They showed the importance of the combined riparian habitats in the midst of a conifer forest and sagebrush community. Each riparian habitat did not have the full complement of all birds. Rather, each small riparian community acted as a component island with its species composition. In the eastern deciduous forest, atmospheric moisture influenced the composite of the breeding bird community (Petit et al. 1985).

Rain, moisture, and/or humidity influenced distribution and reproduction in amphibians and reptiles (Duvall et al. 1982). Some species of frogs must have moist skin in order to breathe.

Tied to the distribution pattern were energy flow and food. Moist areas were likely to have a higher productivity, therefore more food. The concentration of vertebrates in moist habitats meant that they added to the total distribution patterns attracting predators.

Habitat structure has been associated with the presence and diversity of birds and mammals (Shugart et al. 1974). Structure at BCNRA was seen in the coniferous forest from both vertical and horizontal perspectives. Overall, 23.8% of the species of birds observed, 30.1% of the nesting birds, and 24.2% of mammals observed and trapped were in coniferous forests. These habitat types accounted for only 6% of the terrestrial habitats in the study area. Thus, structure of conifer forests appeared to provide habitat for many vertebrates.

Unique aquatic habitats important to fish were the perennial streams that supported salmonids, wetland areas associated with the headwater areas, and gravel-cobble riffles in the headwater rivers. The coldwater streams may support, or could potentially support, native stream fishes such as cutthroat trout. The wetlands associated with headwater streams are probably important spawning and rearing areas for several species, such as the plains killifish, yellow perch, and the centrarchids. The riffle areas are probably spawning sites for over half of the fish species found in the BCNRA. Maintenance of these habitat features will be critical to maintaining current fish species diversity.

The unique islands of aquatic habitat and the forest structure associated with BCNRA provide the diversity of habitat that allows many species to survive there. Influence of people can be seen through the introduction of new species, primarily for sport hunting and fishing, and alteration of habitats that affect native species, primarily through water development and agriculture practices.

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APPENDIX

Habitat association of vertebrates in the BCNRA (* indicates introduced species, ** indicates that species is likely to occur in indicated habitat but not documented within survey).

Species	Habitat association (code from Table 1)
Fish (scientific names according to Baxter and Simon [1970])	
Mountain Whitefish, *Proposopium williamsoni*	7,8
Cutthroat Trout, *Salmo clarki*	6
Rainbow Trout*, *Salmo gairdneri*	6,8
Brown Trout*, *Salvelinus trutta*	6,8
Brook Trout*, *Salvelinus fontinalis*	6,7
Lake Trout*, *Salvelinus namaycush*	8
Lake Chub, *Couesius plumbeus*	6,7,8
Common Carp*, *Cyprinus caprio*	7,8
Sturgeon Chub, *Hybopsis gelida*	7
Flathead Chub, *Hybopsis gracilis*	6,7,8
Fathead Minnow, *Pimephales promelas*	7,8
Longnose Dace, *Rhinichthys cataractae*	6,7,8
River Carpsucker, *Carpoides carpio*	7,8
Longnose Sucker, *Catostomus catostomus*	6,7,8
White Sucker, *Catostomus commersoni*	7,8
Mountain Sucker, *Catostomus platyrhynchus*	8
Shorthead Redhorse, *Moxostoma macrolepidotum*	7,8
Channel Catfish, *Ictalurus punctatus*	7,8
Stonecat, *Noturus flavus*	7,8
Burbot, *Lota lota*	7,8
Plains Killifish, *Fundulus zebrinus*	8
Largemouth Bass*, *Micropterus salmoides*	8
Green Sunfish*, *Lepomis cyanellus*	8
Black Crappie*, *Pomoxis nigromaculatus*	7,8
White Crappie*, *Pomoxis annularis*	8
Yellow Perch*, *Perca flavescens*	7,8
Sauger, *Stizostedion canadense*	7,8
Walleye*, *Stizostedion vitreum vitreum*	7,8
Amphibians (scientific names according to Baxter and Stone [1985])	
Blotched Tiger Salamander, *Ambystoma tigrinum*	3,4,5
Plains Spadefoot Toad, *Scaphiopus bombifrons*	1
Boreal (Western) Toad**, *Bufo boreas*	5
Woodhouse's Toad, *Bufo woodhousei*	4,5
Boreal Chorus Frog, *Pseudacris triseriata*	4,5
Northern Leopard Frog, *Rana pipiens*	4,5
Reptiles (scientific names according to Baxter and Stone [1985])	
Common Snapping Turtle**, *Chelydra serpentina*	4,5
Western Painted Turtle, *Chrysemys picta*	5
Spiny Softshell Turtle, *Trionyx spiniferus*	5,7
Northern Sagebrush Lizard, *Sceloporus graciosus*	1,2,3
Eastern Short-horned Lizard, *Phrynosoma douglassi*	1,2,3
Rubber Boa**, *Charina bottae*	4,5
Yellow-bellied Racer, *Coluber constrictor*	1,2
Bullsnake, *Pituophis melanoleucus sayi*	1,2,3,4
Pale Milksnake, *Lampropeltis triangulum*	1,3,4
Red-sided Gartersnake**, *Thamnophis sirtalis*	4
Wandering Gartersnake, *Thamnophis elegans*	4,5
Western Plains Gartersnake **, *Thamnophis radix*	4
Prairie Rattlesnake, *Crotalus viridis*	1,2,4
Birds (scientific names according to Check-list of North American Birds [1983])	
Common Loon, *Gavia immer*	4,5
Red-throated Loon**, *Gavia stellata*	5
Western Grebe, *Aechmophorus occidentalis*	5
Horned Grebe**, *Podiceps auritus*	5
Eared Grebe, *Podiceps nigricollis*	5
Pied-billed Grebe, *Podilymbus podiceps*	5
White Pelican, *Pelecanus erythrorhynchos*	5
Double-crested Cormorant, *Phalacrocorax auritus*	5
Tundra Swan, *Cygnus columbianus*	5
Trumpeter Swan**, *Cygnus buccinator*	5
Canada Goose, *Branta canadensis*	5
White-fronted Goose**, *Anser albifrons*	5
Snow Goose, *Chen caerulescens*	5
Mallard, *Anas platyrhynchos*	5
Black Duck**, *Anas rubripes*	5
Pintail, *Anas acuta*	5

Gadwall, *Anas strepera*	5
American Wigeon**, *Anas americana*	5
Eurasian Wigeon, *Anas penelope*	5
Northern Shoveler, *Anas clypeata*	5
Blue-winged Teal, *Anas discors*	5
Cinnamon Teal, *Anas cyanoptera*	5
Green-winged Teal, *Anas crecca*	5
Wood Duck, *Aix sponsa*	5
Redhead, *Aythya americana*	5
Canvasback, *Aythya valisineria*	5
Ring-necked Duck, *Aythya collaris*	5
Greater Scaup, *Aythya marila*	5
Lesser Scaup, *Aythya affinis*	5
Common Goldeneye, *Bucephala clangula*	5
Barrow's Goldeneye, *Bucephala islandica*	5
Bufflehead, *Bucephala albeola*	5
Oldsquaw, *Clangula hyemalis*	5
Hooded Merganser, *Lophodytes cucullatus*	5
Red-breasted Merganser, *Mergus serrator*	5
Common Merganser, *Mergus merganser*	5
Ruddy Duck, *Oxyura jamaicensis*	5
Turkey Vulture, *Cathartes aura*	1,2,3,4,5
Goshawk, *Accipiter gentilis*	3
Cooper's Hawk, *Accipiter cooperii*	3,4
Sharp-shinned Hawk, *Accipiter striatus*	3
Northern Harrier, *Circus cyaneus*	1,3,4,5
Rough-legged Hawk, *Buteo lagopus*	1,2,3,4,5
Ferruginous Hawk, *Buteo regalis*	1,2,3,4,5
Red-tailed Hawk, *Buteo jamaicensis*	1,2,3,4,5
Swainson's Hawk**, *Buteo swainsoni*	1,2,4
Broad-winged Hawk**, *Buteo platypterus*	1,5
Golden Eagle, *Aquila chrysaetos*	1,2,4
Bald Eagle, *Haliaeetus leucocephalus*	4,5
Osprey, *Pandion haliaetus*	4,5
Gyrfalcon**, *Falco rusticolus*	1
Prairie Falcon, *Falco mexicanus*	1,2
Merlin, *Falco columbarius*	1,2,3,4,5
American Kestrel, *Falco sparverius*	1,2,3,4,5
Turkey*, *Meleagris gallopavo*	4
Blue Grouse, *Dendragapus obscurus*	3,4
Ruffed Grouse**, *Bonasa umbellus*	1,4
Sharp-tailed Grouse, *Tympanuchus phasianellus*	1
Sage Grouse, *Centrocercus urophasianus*	1
Chukar*, *Alectoris chukar*	2
Ring-necked Pheasant*, *Phasianus colchicus*	1,3,4
Grey Partridge*, *Perdix perdix*	1
Great Egret**, *Casmerodius albus*	1,4,5
Snowy Egret, *Egretta thula*	5
Cattle Egret*, *Bubulcus ibis*	5
Great Blue Heron, *Ardea herodias*	5
Black-crowned Night Heron, *Nycticorax nycticorax*	5
American Bittern, *Botaurus lentiginosus*	5
White-faced Ibis, *Plegadis chihi*	5
Sandhill Crane, *Grus canadensis*	1
Virginia Rail, *Rallus limicola*	5
Sora, *Porzana carolina*	5
Yellow Rail**, *Coturnicops noveboracensis*	5
American Coot, *Fulica americana*	5
American Avocet, *Recurvirostva americana*	5
Black-necked Stilt, *Himantopus mexicanus*	5
Mountain Plover, *Charadrius montanus*	1
Lesser Golden Plover**, *Pluvialis dominica*	5
Black-bellied Plover**, *Pluvialis squatarola*	5

Semipalmated Plover**, *Charadrius semipalmatus*	1,5
Killdeer, *Charadrius vociferus*	5
Marbled Godwit**, *Limosa fedoa*	5
Hudsonian Godwit**, *Limosa haemastica*	5
Long-billed Curlew, *Numenius americanus*	1,4,5
Greater Yellowlegs, *Tringa melanoleuca*	5
Lesser Yellowlegs, *Tringa flavipes*	5
Solitary Sandpiper, *Tringa solitaria*	5
Upland Sandpiper, *Bartramia longicauda*	1
Buff-breasted Sandpiper**, *Tryngites subruficollis*	5
Stilt Sandpiper, *Calidris himantopus*	5
Willet, *Catoptrophorus semipalmatus*	5
Spotted Sandpiper, *Actitis macularia*	5
Long-billed Dowitcher, *Limnodromus scolopaceus*	5
Wilson's Phalarope, *Phalaropus tricolor*	5
Red-necked Phalarope, *Phalaropus lobatus*	5
American Woodcock**, *Scolopax minor*	4
Common Snipe, *Gallinago gallinago*	5
Pectoral Sandpiper**, *Calidris melanotos*	5
Red Knot**, *Calidris canutus*	5
Dunlin, *Calidris alpina*	5
Sanderling, *Calidris alba*	5
Baird's Sandpiper**, *Calidris bairdii*	5
Least Sandpiper, *Calidris minutilla*	5
Western Sandpiper, *Calidris mauri*	5
California Gull, *Larus californicus*	5
Ring-billed Gull, *Larus delawarensis*	5
Franklin's Gull, *Larus pipixcan*	5
Bonaparte's Gull, *Larus philadelphia*	5
Common Tern, *Sterna hirundo*	5
Forster's Tern, *Sterna forsteri*	5
Caspian Tern**, *Sterna caspia*	5
Black Tern, *Chlidonias niger*	5
Rock Dove, *Columba livia*	1,2,3,4,5
Mourning Dove, *Zenaida macroura*	1,2,3,4,5
Yellow-billed Cuckoo**, *Coccyzus americanus*	4
Black-billed Cuckoo, *Coccyzus erythropthalmus*	4
Screech Owl, *Otus kennicottii*	1,2,3,4,5
Great Horned Owl, *Bubo virginianus*	1,2,3,4,5
Long-eared Owl, *Asio otus*	1,2,3,4,5
Short-eared Owl, *Asio flammeus*	1,2,3,4,5
Snowy Owl, *Nyctea scandiaca*	1,2,3,4,5
Northern Hawk-Owl**, *Surnia ulula*	3,4
Burrowing Owl, *Athene cunicularia*	1,4
Northern Saw-whet Owl, *Aegolius acadicus*	1,4
Common Poorwill, *Phalaenoptilus nuttallii*	1
Common Nighthawk, *Chordeiles minor*	1,2,3,4,5
Chimney Swift**, *Chaetura pelagica*	1,2,3,4,5
White-throated Swift, *Aeronautes saxatalis*	1,2,3,4,5
Ruby-throated Hummingbird**, *Archilochus colubris*	4
Broad-tailed Hummingbird, *Selasphorus platycercus*	4
Calliope Hummingbird, *Stellula calliope*	4
Rufous Hummingbird**, *Selasphorus rufus*	1,3,4
Belted Kingfisher, *Ceryle alcyon*	5
Common Flicker, *Colaptes auratus*	3,4
Red-headed Woodpecker, *Melanerpes erythrocephalus*	4
Lewis' Woodpecker, *Melanerpes lewis*	4

Yellow-bellied Sapsucker, *Sphyrapicus varius*	4
Williamson's Sapsucker**, *Sphyrapicus thyroideus*	3
Hairy Woodpecker, *Picoides villosus*	3,4
Downy Woodpecker, *Picoides pubescens*	3,4
Black-backed Woodpecker**, *Picoides arctus*	3
Three-toed Woodpecker**, *Picoides tridactylus*	3
Eastern Kingbird, *Tyrannus tyrannus*	1,4
Western Kingbird, *Tyrannus verticalis*	1,4
Cassin's Kingbird, *Tyrannus vociferans*	1,2,3,4
Say's Phoebe, *Sayornis saya*	1
Willow Flycatcher, *Empidonax traillii*	4
Least Flycatcher, *Empidonax minimus*	4
Hammond's Flycatcher, *Empidonax hammondii*	3
Dusky Flycatcher, *Empidonax oberholseri*	1,2,4
Western Flycatcher, *Empidonax difficilis*	4
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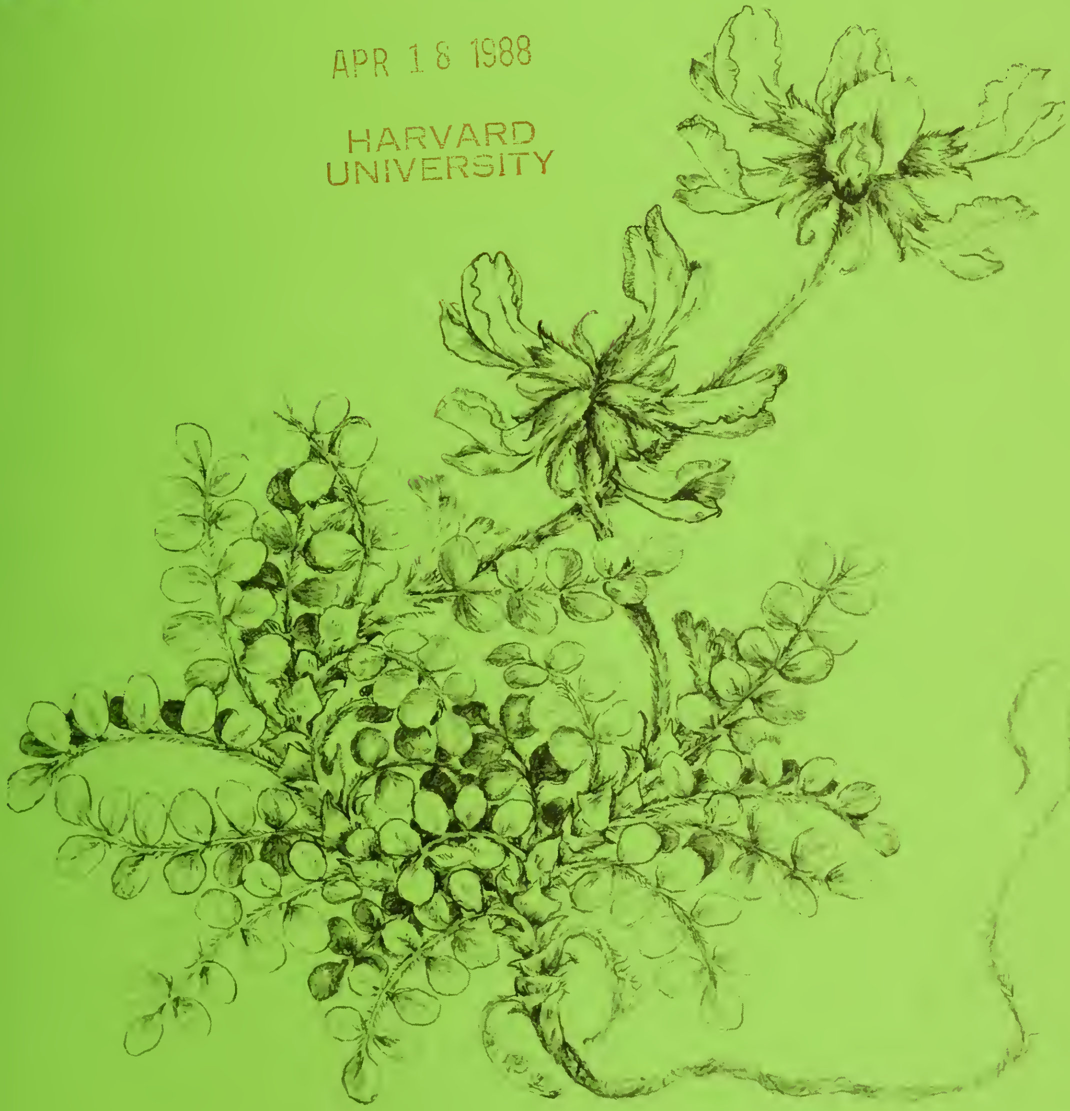

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RECORDS OF EXOTIC FISHES FROM IDAHO AND WYOMING

Walter R. Courtenay, Jr.[1], C. Richard Robins[2],
Reeve M. Bailey[3], and James E. Deacon[4]

ABSTRACT.—One exotic poeciliid (*Xiphophorus helleri*) and two cichlids (*Cichlasoma nigrofasciatum* and *Tilapia mossambica*) are recorded as recently established in thermal springs and their outflows in southern Idaho. *Misgurnus anguillicaudatus* was collected and is considered as established in the Boise River system. *Poecilia mexicana* and juvenile hybrid tilapias are recorded from the Bruneau River at Bruneau Hot Springs, Idaho. A reproducing population of *X. helleri* was found in a spring within the boundaries of Grand Teton National Park, Wyoming. *Poecilia reticulata*, previously reported from one spring each in Idaho and Wyoming, is recorded from a second spring outflow in Idaho.

Simpson and Wallace (1978) and Baxter and Simon (1970) listed the guppy, *Poecilia reticulata* Peters, as the only tropical exotic fish established in Idaho and Wyoming. It was known from a thermal spring in the Little Lost River Valley north of Howe, Butte County, Idaho (Linder 1964), and Kelly Warm Spring, Teton County, Wyoming (within Grand Teton National Park).

As part of a continuing investigation of established exotic fishes in the United States, we (WRC, CRR, RMB) collected fishes from two warm springs in southern Idaho on 7 September 1985, a chilly, rainy day, air temperature 11 C. The first collection site was Warm Springs Creek, Clark County, T11N, R32E, 17.9 km north of Idaho State Highway 22, about 0.5 km from the spring head; temperature was 25.5 C at the site and 27.7 C at the spring. The second site was Barney Hot Spring, Custer County, T12N, R25E, Little Lost River Valley, 67 km north-northwest of Howe. Temperature in the spring was 27 C in shallows along the perimeter.

Two additional collections of fishes were made by WRC and JED in southwestern Idaho on 26 and 27 September 1986, respectively. The first was in a heavily vegetated irrigation ditch, the Harton Davis Canal, Ada County, T4N, R1W, along the northeastern edge of Eagle State Park; canal temperature was 17 C. The second was made in the Bruneau River below the Blackstone Grasmere Road bridge, Bruneau Hot Springs, Owyhee County, T7S, R6E; water temperature was 15 C in the river, 20–22 C in the collecting area, and 23 C in a thermal inflow just upstream of the collection site.

Fishes were sampled by WRC in Kelly Warm Spring, 1.6 km north-northeast of the town of Kelly, Teton County, Wyoming, T42N, R115W, on 23 July 1984. Additional observations were made from the surface on 13 September 1985. Temperature in this spring is nearly constant, 25–27 C (P. S. Hayden, personal communication).

METHODS AND MATERIALS.—Fishes were sampled in each spring system and the irrigation ditch with galvanized minnow traps (44 × 25 cm, 6.4-mm mesh). Canned dog food was used in traps as bait in the two Idaho springs, and bread was used at the Wyoming site; traps placed in the irrigation ditch were unbaited. Trapping time was 30 minutes in Warm Springs Creek, about 45 minutes in the irrigation ditch, and one hour in the other springs. Fine mesh dipnets also were used at the two Idaho springs and their outflows, and nylon minnow seines (4.6 × 1.8 m, 6.4-mm mesh) were used in the Bruneau River. Approximately 75% of the Kelly Warm Spring pool was observed underwater using face mask and snorkel during the trapping period; additional surface observations were made on 13 September 1985 from the pool perimeter with polaroid glasses.

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Standard length measurements were taken to the nearest mm with dial calipers. Specimens are deposited in the collections of Florida Atlantic University (FAU), University of Michigan Museum of Zoology (UMMZ), and University of Nevada at Las Vegas (UNLV).

Results

Idaho

Fishes collected in the narrow (about 0.75–1.5 m) Warm Springs Creek included 120 guppies (13–36 mm SL, UMMZ 213369 and FAU WRC-ID-1) and 121 green swordtails, *Xiphophorus helleri* Heckel (19–66 mm SL, UMMZ 213370 and FAU WRC-ID-1). No native fishes were seen or collected. The spring head and its immediate outflow doubtless provide thermal refuge during winter months.

In Barney Hot Spring and the upper end of Barney Creek, we collected 29 guppies (13–27 mm SL, UMMZ 213371 and FAU WRC-ID-2), 95 green swordtails (14–36 mm SL, UMMZ 213372 and FAU WRC-ID-2), 19 amelanic convict cichlids, *Cichlasoma nigrofasciatum* (Günther) (15–92 mm SL, UMMZ 213373 and FAU WRC-ID-2), and 142 Mozambique tilapia, *Tilapia mossambica* (Peters) (19–78 mm SL, UMMZ 213374 and FAU WRC-ID-2). Within the spring, all fishes were collected from and observed in the perimeter shallows. Guppies were not as numerous as reported by Linder (1964) and were rare in the pond. Tilapia nests were located primarily at the southern end of the approximately 15-m–diameter spring pool, near the outflow (Barney Creek). Guppies, swordtails, and a few convict cichlids were found in the creek, the cichlids only near the pond outflow. No other fishes were observed or collected at this location. Apparently the introduction of cichlids has resulted in the near elimination of guppies from the pond.

One Oriental weatherfish, *Misgurnus anguillicaudatus* (Cantor) (102 mm SL, UNLV 1951), was collected from Harton Davis Canal near Eagle.

A pair of shortfin mollies, *Poecilia mexicana* Steindachner, (♂ 35 and ♀ 40 mm SL, UMMZ 213783) and 10 juvenile tilapias (17–23 mm SL, UNLV 1952), probably hybrids of *Tilapia mossambica* × *T. hornorum* Trewavas, were captured in the Bruneau River at Bruneau Hot Springs. The collection site was adjacent to a thermal inflow (23 C) that drains from ponds of a nearby aquaculture facility. In addition to the two exotic species, common carp, *Cyprinus carpio* Linnaeus, and orange-spotted sunfish, *Lepomis humilis* (Girard) were taken. Native fishes in the area included redside shiner, *Richardsonius balteatus* (Richardson) (abundant), chiselmouth, *Acrocheilus alutaceus* Agassiz & Pickering, northern squawfish, *Ptychocheilus oregonensis* (Richardson), and large-scale sucker, *Catostomus macrocheilus* Girard (all common). Collections were made in water to 1 m in depth.

Wyoming

Sixty-five guppies (18–35 mm SL, FAU WRC-WY-1) and 203 green swordtails (15–68 mm SL, FAU WRC-WY-1) were collected in minnow traps from Kelly Warm Spring. Also collected and released were 37 Utah chubs, *Gila atraria* (Girard), and 2 speckled dace, *Rhinichthys osculus* (Girard).

Observations using face mask and snorkel showed that Utah chubs were common over open areas and near vegetation in the southwestern part of the Y-shaped spring pool (approximately 110 × 24 m; P. S. Hayden, personal communication). Speckled dace were observed primarily around spring boils over open sand and fine gravel, away from the pool perimeter. Green swordtails were common in the perimeter shallows and abundant in aquatic vegetation along the southeastern shore; guppies were also concentrated at the latter site. Both exotics showed the same distribution when the pool was observed from the surface in 1985.

Discussion

These records of green swordtails are the first for Idaho and Wyoming, and those of Oriental weatherfish, shortfin mollies, convict cichlids, Mozambique tilapias, and hybrid tilapias are the first for Idaho. Introductions of guppies, the other tropical exotic fishes except hybrid tilapias, and the Oriental weatherfish resulted from releases of aquarium fishes. Juvenile hybrid tilapias escaped from a culture facility. Cichlids were reported to have been released in Kelly Warm Spring, Wyoming (P. S. Hayden, personal communication), but none was observed or collected.

No native fishes were collected at the Idaho springs. That native species occupied those waters in recent times is doubtful. Barney Hot Spring is isolated from the Upper Snake River by the Lost River Sinks downstream, and its outflow sinks below the surface before entering the Little Lost River (Linder 1964). Moreover, there is an absence of warm-water fishes. Simpson and Wallace (1978) indicated only salmonids and shorthead sculpin, *Cottus confusus* Bailey & Bond, as native in the Little Lost River drainage of Idaho.

The Oriental weatherfish was the only fish collected from the irrigation ditch at Eagle State Park. V. K. Moore (personal communication) reported the presence of an unidentified "Chinese loach" in the Boise River system and added that it had been there for several years, with a few specimens having been captured. Although we collected only one specimen, we consider the species as established. Self-sustaining populations of this exotic are also present in California and Michigan (Courtenay et al. 1986).

The capture of a pair of shortfin mollies in the Bruneau River in the same shallow, vegetated, warm inflow area of the river from which the juvenile *Tilapia* were collected may indicate that this species is established immediately upstream in Indian Bathtub, an area of inflowing thermal water. Poeciliids have been reported previously from Bruneau Hot Springs (V. K. Moore, personal communication), and we believe Indian Bathtub is the most likely site where they were seen or collected. Shortfin mollies are established in California and Nevada (Courtenay et al. 1986). The species was also reported as established in Trudau Pond, Madison County, Montana (Brown 1971), but no specimens were collected there in September 1985.

Tilapia culture in thermal waters in southern Idaho has expanded recently. Blue tilapia, *Tilapia aurea* (Steindachner), have been cultured for several years in Hagerman Valley, Twin Falls County, and may have established following escape in the Snake River near natural thermal inflows (V. K. Moore, personal communication). A similar situation occurred in Pennsylvania where escaped blue tilapia established in the lower Susquehanna River and now overwinter near power plant thermal effluents (Skinner 1984, 1986). The culture facility near Bruneau Hot Springs seemed to be of recent construction. The "red" tilapias being cultured there appear to be a hybrid that is being used increasingly in aquaculture operations in Idaho and elsewhere. If this hybrid is fertile, as many tilapia hybrids are, we predict that it will become established near thermal inflows in the Bruneau River.

Kelly Warm Spring drains into the upper Snake River via Mormon Row Ditch into downstream Ditch Creek. A second irrigation ditch, Savage Ditch, permits water to be diverted from the Gros Ventre River into Mormon Row Ditch, just below the outflow from Kelly Warm Spring. The spring was excavated in the late 1940s for the purpose of increasing flow into those ditches (P. S. Hayden, personal communication). A flow-control structure separates the spring pool from the ditches.

Baxter and Simon (1970) recorded Utah chubs, speckled dace, and Utah suckers, *Catostomus ardens* Jordan & Gilbert, from Kelly Warm Spring. Utah chubs and suckers live in warm spring outflows (Jordan 1891, Linton 1893, R. D. Jones, personal communication). Speckled dace commonly inhabit warm springs (Sigler and Miller 1963).

No Utah suckers were collected or observed in Kelly Warm Spring in July 1984. Although suckers are not easily trapped, adults are generally readily observed underwater (Courtenay et al. 1985). Suckers may have been present near the outflow structure, the only area of the spring pool not observed with mask and snorkel. P. S. Hayden (personal communication) indicated that they were seen in the pool some five to six years prior to 1984. He also stated that the structure is opened periodically and, depending on outflow volume and speed, could permit entry from the ditches.

Most of the exotic fishes reported herein are restricted to warm waters and do not appear to represent a threat to native fishes in Idaho or Wyoming. Nevertheless, they serve as additional examples of unauthorized introductions, even in areas remote to civilization and, in one case, within a national park. Obviously, those persons introducing these tropical fishes go to considerable lengths to establish them. In the Boise and Bruneau rivers, and in Kelly Warm Spring, sympatry with the native fauna could lead to adverse consequences. Introductions in similar situations in other states have been implicated in the decline and extinction of native fishes (e.g., Miller 1961, Minckley and Deacon 1968, Deacon et al. 1964, Lachner et al. 1970, Deacon 1979, Courtenay and Deacon 1982, Courtenay et al. 1985, Heckmann et al. 1987).

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REVISION OF *SAHNIOCARPON HARRISII* CHITALEY & PATIL BASED ON NEW SPECIMENS FROM THE DECCAN INTERTRAPPEAN BEDS OF INDIA

E. M. V. Nambudiri[1], William D. Tidwell[2], and Shya Chitaley[3]

ABSTRACT.—New specimens of *Sahniocarpon harrisii* Chitaley & Patil were collected from the Deccan Intertrappean beds at Mahgaon Kalan in central India. These specimens form the basis for this reinvestigation of the species and an emended diagnosis. A tuberculated seed coat, a chalazal haustorium, and the bitegmic nature of the testa can be observed in the new specimens. These features were not included in the original description. Although the extant genera of Clusiaceae and *Sahniocarpon* are not similar in all aspects, they are close enough to tentatively assign *Sahniocarpon* to this tropical family.

Well-preserved plant fossils, a majority of them angiospermic, have been noted from the Deccan Intertrappean beds exposed at Mohgaon Kalan in central India. The fossil plants from this locality include woods, roots, leaf impressions, flowers, and fruits. Petrified wood is the predominant fossil material from these beds, whereas fruiting structures are rare.

The first fruiting structure documented from the Mohgaon Kalan locality was *Enigmocarpon parijai*, a multilocular, many-seeded loculicidal capsule described by Sahni (1943). Since this publication, only a few additional dicot fruits have been reported from this locality by later workers. Jain (1964) and Nambudiri (1969) described fossil species of *Indocarpa* that were related to modern genera of Guttiferae, and two new genera of fossil fruits with malvaceous affinities were detailed by Chitaley and Nambudiri (1973) and Chitaley and Sheikh (1971).

The only other dicot fruit known from the Deccan Intertrappean series at this locality is *Sahniocarpon harrisii* Chitaley & Patil (1971). Additional specimens of this species collected by EMVN from the same Intertrappean beds exposed at Mohgaon Kalan, Chhindwara district, Madhya Pradesh, India (Fig. 1), are described here. The reinvestigation and subsequent emended diagnosis of *Sahniocarpon* are based on these new specimens.

The age of the Deccan Traps has long been a subject of much debate. Geologists, such as Krishnan (1969) and Wadia (1966), generally regard the Deccan volcanism as an Upper Cretaceous activity. This view was held by many researchers until Crooksank (1937) and Sahni (1937) reviewed the paleontological and geochemical data and, based upon their findings, suggested an Early Tertiary age for these beds. Plant fossils such as *Nipadites* (*Nypa*) (Rode 1933), the freshwater alga, *Chara* (Malcolmson 1837, Rao and Rao 1935), and palms are indicative of an Early Tertiary age (Sahni 1937). Because of mass extinctions associated with the iridium anomaly, the Cretaceous-Tertiary boundary has recently received much attention. Through this research much radiometric data have been generated concerning the Deccan Traps. The Potassium-Argon dates from these rocks suggest that the volcanic activity spanned a considerably longer time period than originally thought. Alexander (1981) reviewed the K-Ar dates for the Deccan Traps in the Chhindwara area, the collecting locality for the *Sahniocarpon* fruits, and suggested an age of 47 Ma. for the volcanic Trap strata. This is in agreement with Sahni's original interpretation that the Intertrappean beds at Mohgaon Kalan, Chhindwara district, is of Early Tertiary age. Paleomagnetic studies of the Deccan Traps note a reversely magnetized lower and a normally magnetized upper traps (Athavale et al. 1963, Clegg et al. 1956, Verma and Pulliah 1967). Geomagnetic field reversal, an Upper Cretaceous phenomenon, is recognized in both continental and oceanic sequences and is easily discerned in the North Indian Ocean

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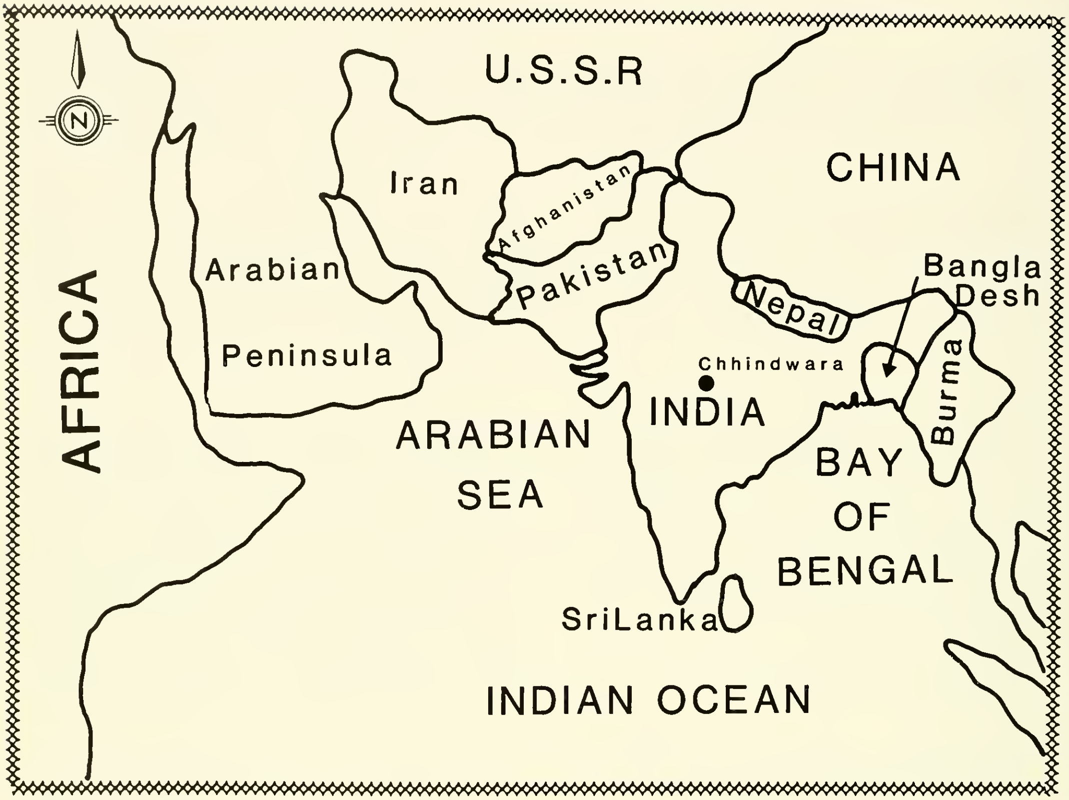


Fig. 1. The regional map showing the position of the Indian subcontinent. The Mohgaon Kalan locality in Chhindawar district is indicated.

sequence (Scalter and Fischer 1974). However, data accumulated from plant fossils suggest that the Intertrappean beds in the Chhindwara area are Paleocene to Early Eocene in age.

SYSTEMATIC PALEOBOTANY

Sahniocarpon harrisii Chitaley & Patil (1971)

SPECIFIC DIAGNOSIS (emended).—Fruit round to oval (6.5 × 7.5 mm), pentalocular, septicidal capsule; pericarp (0.85–1.6 mm thick) divided into outer zone (0.35–0.7 mm) of fleshy or hard tissues (each cell 27–36 μm in size) and an inner zone of fleshy or aerenchymatous cells; dehiscence along the septae, septae five, meeting at the center of the fruit; placentation axile; each locule single-seeded; seeds obovate, anatropous, with 3 attenuated, chalazal outgrowths; seeds endospermic, bitegmic, testa (115 μm wide), tuberculated; embryo axis (3071 × 629 μm) with a radicle towards the micropylar end, embryonic leaves, plumule and a chalazal haustorium at the chalazal end; seeds attached to the base of the axile placentum by a short funicle (592 μm long).

DESCRIPTION

This permineralized fruit (7 × 7.2 mm) is a round to oval, pentalocular, septicidal capsule (Figs. 2, 3). The dry pericarp (1.5 mm thick) is differentiated into an outer zone of comparatively hard tissues and an inner fleshy zone (Fig. 18). The locules are separated by five septae (Figs. 5, 6). At the distal end of the fruit, the locules split along septal margins (septicidal dehiscence; Fig. 4). A single, anatropous seed, completely infilling the locule (Fig. 9), is added to the base of the axile placentum by a short (592 μm long) funicle (Fig. 14). Each seed is obovate with a narrow micropylar end and a broad chalaza (Fig. 5). At the chalazal end, these seeds have three trian gular, attenuated, stony outgrowths (Figs. 4,

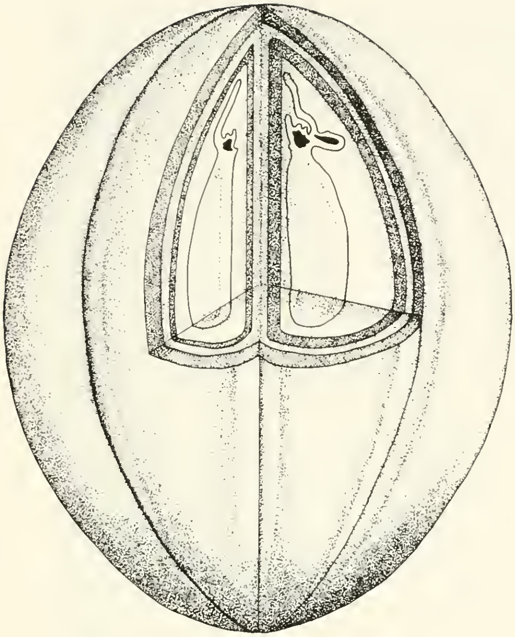


Fig. 2. Reconstruction of *Sahniocarpon harrisii* Chitaley & Patil (not to scale).

5). The testa is hard and bitegmic, derived from outer and inner integuments (Figs. 7, 10, 12, 15). The outer integument is tuberculated by fleshy outgrowths arising from the testa (Fig. 12). The cotyledonary cells are poorly preserved. The embryo axis (3071 μm long and 629 μm wide) is comparatively large and is differentiated into a radicle, located at the micropylar end, and a plumule at the chalazal end (Fig. 9). Embryonic leaves, arising from the plumule and formed by the differentiation of the shoot apex, are clearly visible. An elongated haustorium is attached to the embryo at the chalazal end (Fig. 9).

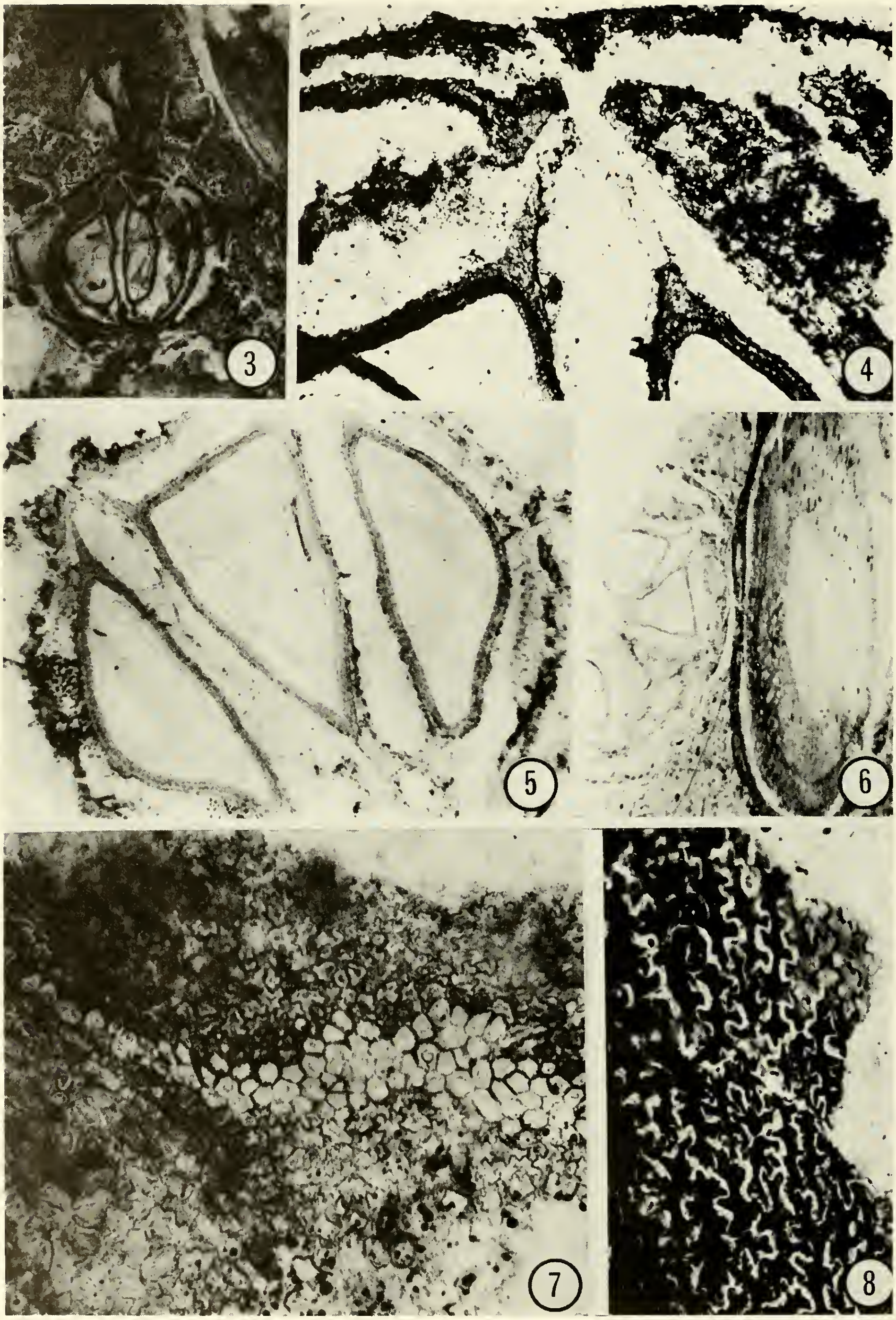
PERICARP.—The pericarp is differentiated into outer and inner layers (Fig. 18). The outer pericarp is formed of polygonal, thick-walled, compactly arranged cells (mean diameter of 35.5 μm). This tissue is covered by a single-layered epidermis, composed of rectangular cells (12 μm). This epidermis is occasionally covered by cuticle. Conversely, cells of the inner pericarp (24.2 μm) are formed exclusively of thin-walled, round to oval, or polygonal cells. Vascular bundles traverse the inner pericarp.

VASCULATURE OF THE FRUIT.—The main lateral vascular bundle can be traced throughout the inner pericarp (Fig. 13). This vascular bundle in transverse section (126 μm × 97 μm) shows two main metaxylem vessel elements (20 μm) and four to five protoxylem vessel elements (14 μm). A layer of sclerotic tissues surrounds each bundle (Fig. 13). This main vasculature of the fruit supplies branches into the septae, which are composed of parenchymatous cells. Longitudinally oriented vessel elements of the septum have spiral wall thickenings (Fig. 11). Although cells of the phloem tissue are not easily discernible, it is assumed that the thin-walled cells in the vascular bundles are functional phloem cells.

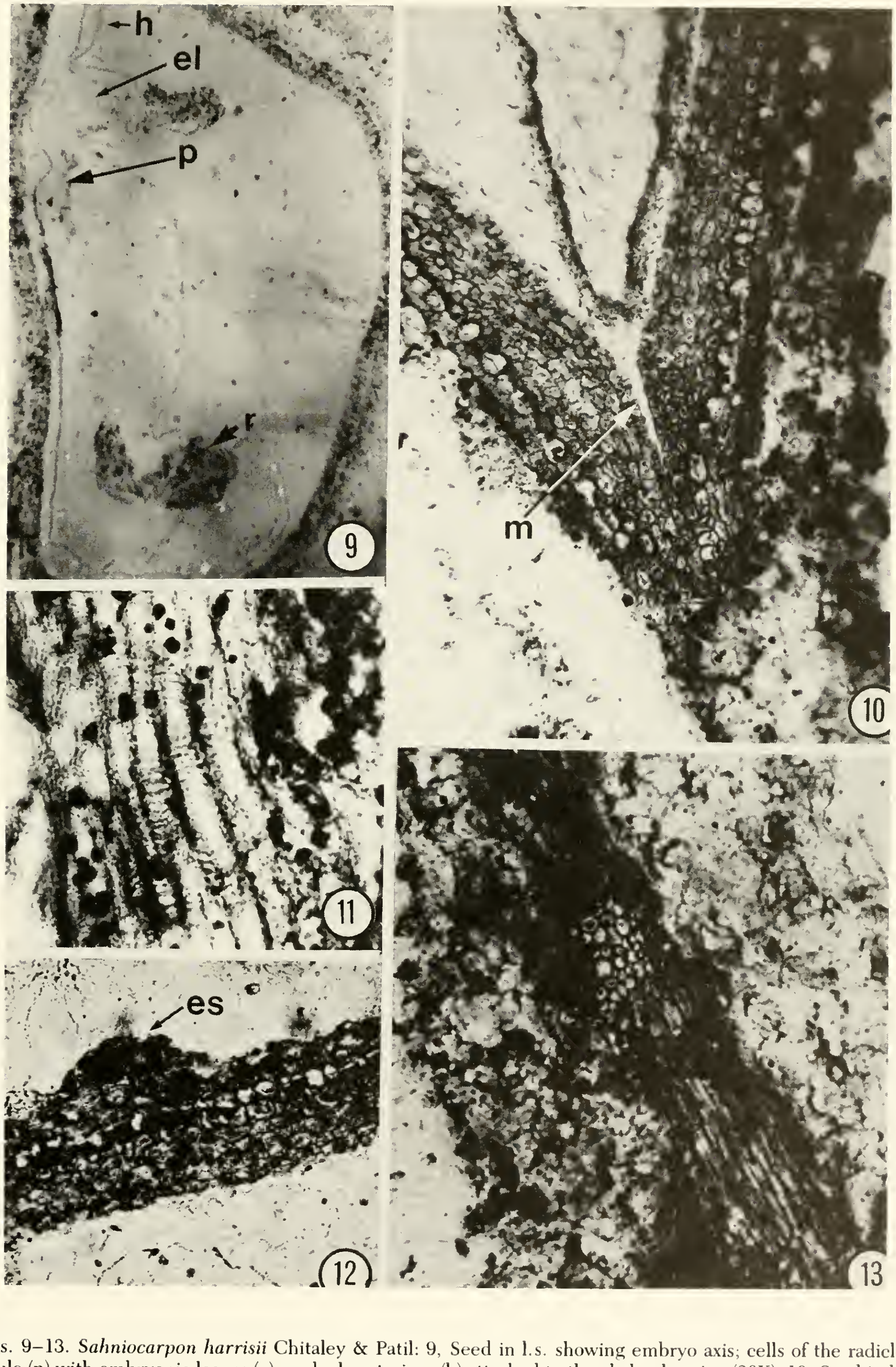
SEEDS.—The testa (115 μm wide) is formed from the outer and inner integuments of the bitegmic ovules (Figs. 7, 10, 12, 15). Two to five layers of highly thick-walled cells form the outer testa. Apparently due to attenuated appendages, the testa attains a maximum thickness at the chalazal end. Cells of these appendages are exclusively thick walled. The inner testa is comparatively less sclerotic. Eight to ten layers of round to polygonal cells form the inner testa. A distinct layer of barrel-shaped cells (31 μm × 16.8 μm), separating the outer from the inner testa (Figs. 7, 10, 12, 15), is developed from the innermost layer of the outer integument. Outer walls of these cells are thin walled, whereas the inner and tangential walls are thickened (Fig. 15). Cells of the testa in surface view are elongated with sinuous cell walls (Fig. 8).

Round to oval, fleshy outgrowths (Fig. 12), similar to elaiosomes (Esau 1979), give the seeds a tuberculated appearance. These tubercles are formed of thin-walled, polygonal cells. Like septal cells, cells of the elaiosomes have undergone considerable degradation due to the attack of fungi. In fact, fungal mycelia and spores are clearly visible inside the fruit and seeds. The anatropous nature of the seeds is ascertained by the presence of a micropyle (14 μm wide) located near the funicle (Figs. 10, 14). Both outer and inner integuments take part in the formation of the micropylar duct. Vascular bundles are clearly visible at the chalaza.

EMBRYO.—The embryo (3071 μm × 629 μm) completely fills the seed cavity. Cells of this embryo are polygonal (wherever preserved), thin walled, and parenchymatous



Figs. 3–8. *Sahniocarpon harrisii* Chitaley & Patil: 3, Fruit in l.s. showing septicidal dehiscence, nature of pericarp, seed coat, and embryo axis (4.5X); 4, Fruit in l.s. showing dehiscence at the distal end (26X); 5, Fruit in l.s. showing three seeds; the central seed is attached to the base of the axile placentum by a short funicle (15X); 6, Fruit in t.s. shows each locule containing a single seed (7X); 7, Testa in oblique section showing the outer and inner integuments (140X); 8, Cells of testa in surface view (300X).



Figs. 9–13. *Sahniocarpon harrisii* Chitaley & Patil: 9, Seed in l.s. showing embryo axis; cells of the radicle (r), plumule (p) with embryonic leaves (e), and a haustorium (h) attached to the chalazal region (30X); 10, Seed in l.s. to show the micropyle (m) formed of outer and inner integuments (130X); 11, Vascular bundle in the pericarp showing vessel elements with helical thickenings (20X); 12, Testa in l.s. showing elaiosomes (es) (250X); 13, Pericarp in l.s. showing vascular bundles (120X).

(Figs. 9, 16). Cells of the radicle, also parenchymatous, are well preserved.

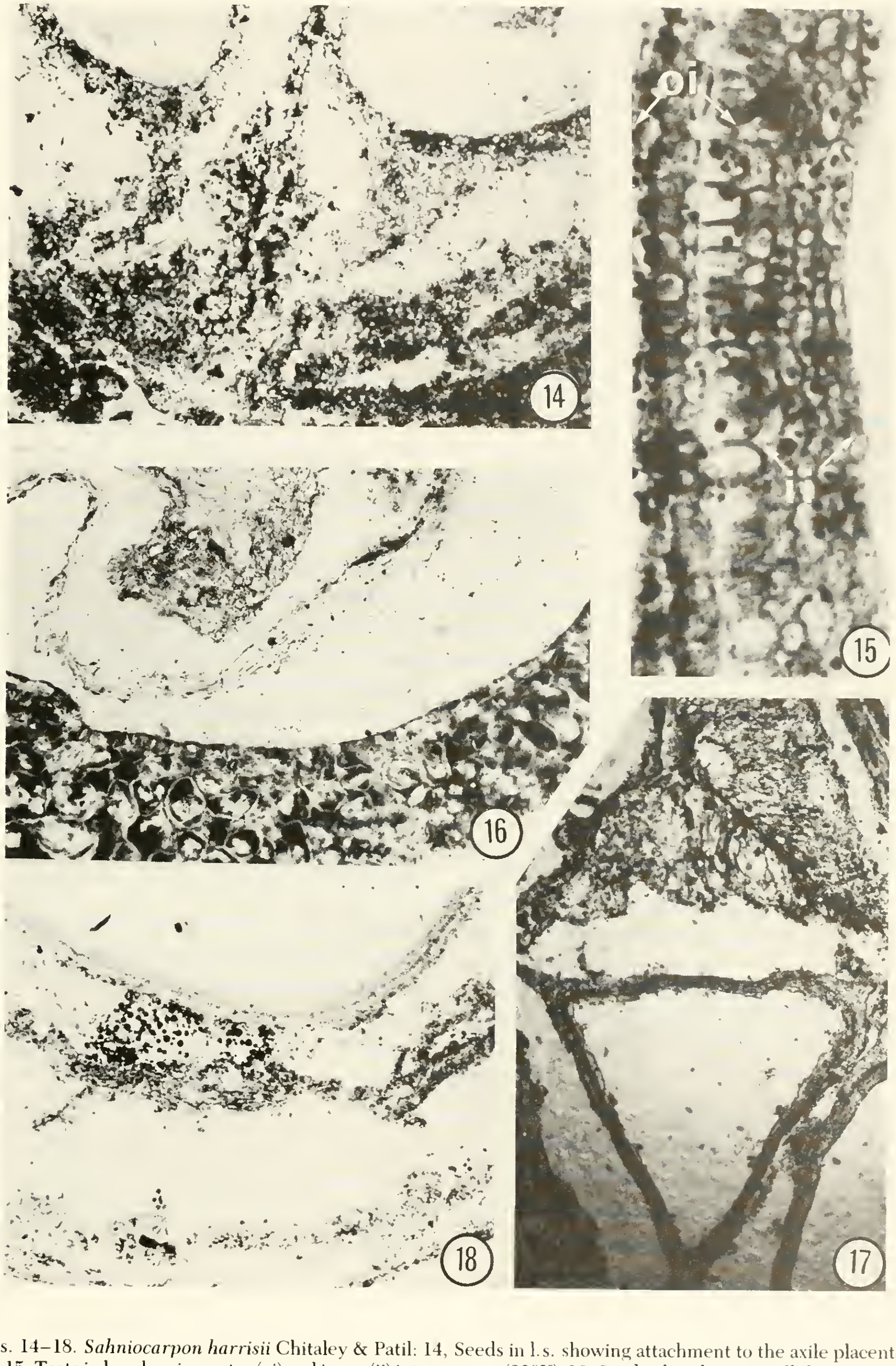
COMPARISONS AND AFFINITIES

On comparison with the several dicotyledonous fruits from the Deccan Intertrappean series, it is clear that these permineralized fruit specimens are, in fact, *Sahniocarpon harrisii*. Sahni (1943) described a loculicidal capsule, *Enigmocarpon parijai*, having lythraceous and sonneratiaceous affinities. *Sahniocarpon harrisii* differs from *Enigmocarpon parijai* in having single-seeded locules and also in being a septicidal rather than a loculicidal capsule. *Enigmocarpon* has several seeds per locule. In addition, the hypostase tissue in *Enigmocarpon* is absent in *Sahniocarpon harrisii*. The other dicotyledonous fruits known from these Intertrappean beds are *Indocarpa intertrappea* Jain (1964), *I. mahabalei* Nambudiri (1969), *Harrisocarpon sahnii* Chitaley & Nambudiri (1973), and *Daberocarpon gerhardii* Chitaley & Sheikh (1971). *Daberocarpon gerhardii* is a multilocular fruit with a single seed in each locule. Chitaley and Sheikh (1971) suggested affinities for this genus of fruit with such malvaceous genera as *Abutilon indicum*, *Malva parsiflora*, *Malva sylvestris*, *Malvastrum* sp., *Sida cordifolia*, and *Sida rhombifolia*.

Harrisocarpon sahnii is also a septicidal capsule but contains two seeds per locule. *Sahniocarpon harrisii* is different from both species of *Indocarpa* in having a stony seed coat as compared to the sarcotesta in *Indocarpa*. Moreover, *Indocarpa* is a multiseeded, septifragal capsule.

Chitaley and Patil (1971) stated that the *Sahniocarpon* pericarp is fleshy with aerenchymatous cells in the inner layers of the pericarp. The specimens described here, however, indicate that the pericarp is divisible into an outer zone of hard tissues and an inner zone of fleshy tissues. The pericarp in these new specimens lacks air chambers. Such differences are, perhaps, induced by ecological conditions and should not be used for discriminating at specific levels. The abundance of aerenchymatous tissue in the specimens described by them suggests that the parent plants were perhaps growing around several small lakes that formed an integral part of the Deccan landscape during the Intertrappean time. Another feature of interest is the nature of the testa. Chitaley and Patil (1971) mentioned that the testa is composed of three zones, the outer and inner zones of thin-walled parenchymatous cells and a central zone of elliptical cells with radial wall thickenings. Except for the sclerotic outer and inner testa, the structure of the seed coat as described by Chitaley and Patil (1971) is somewhat similar to the new specimens. A layer of barrel-shaped cells, separating the outer and inner testa, is the innermost layer of the outer integument. Ontogenetically, bitegmic seeds of Cruciferae develop a similar structure in their testa (Vaughn and Whitehouse 1971). Esau (1979) suggested that if subepidermal parenchyma is present in the outer integument, they are either crushed or become thick walled. Such thick-walled cells may have formed during the development of the seed coat in these new specimens of *Sahniocarpon*. The seeds are anatropous in both *Sahniocarpon* and our new specimens, but in the latter the seeds are attached to the base of the axile placentum by a funicle. For purpose of clarity, we have used the term funicle rather than raphe (Chitaley and Patil 1971). The raphe is a ridge formed by adnation of the funiculus with the ovule (Esau 1979). While such minor differences exist between the type specimens of *Sahniocarpon harrisii*, it is evident that the specimens described here belong to the genus *Sahniocarpon*. There are features in the new specimens that were not originally described by Chitaley and Patil (1971) for *Sahniocarpon harrisii*, such as, the tuberculated seed coat, the chalazal haustorium, and the bitegmic nature of the testa. The specific diagnosis of the *Sahniocarpon harrisii* has been, therefore, emended to include these additional characteristics.

Several features present in the *Sahniocarpon* fruit may be primitive. The majority of angiosperms (84.6% of dicotyledons; Davis 1966) have anatropous ovules. Although Sporne (1974) suggested that orthotropous ovules should be regarded primitive, Eames (1961) and Takhtajan (1969) noted that orthotropous ovules were derived from the anatropous condition and should be considered advanced. There is a general agreement, however, that bitegmic ovules are primitive in comparison with the unitegmic ovules (Joshi 1939, Maheswari 1950). Many angiospermous



Figs. 14–18. *Sahniocarpon harrisii* Chitaley & Patil: 14, Seeds in l.s. showing attachment to the axile placentation (42X); 15, Testa in l.s. showing outer (oi) and inner (ii) integuments (320X); 16, Seed in l.s. showing cellular nature of the embryo axis (100X); 17, Seeds in t.s.; the seed at the top of the picture is in surface view (26X); 18, Fruit in l.s. showing pericarpic tissues (35X).

TABLE 1. Range of characters in subfamilies Clusioideae and Hypericoideae (based on information in Corner 1976, Davis 1966, Lawrence 1951).

CHARACTER	CLUSIOIDEAE	HYPERICOIDEAE
FRUIT		
Nature of fruit	Capsule, berry, or drupe	Capsule or berry
Number of locules	1–many	3–5
Number of ovules	1–many	Numerous
Orientation of ovules	Usually straight	Straight or curved
Nature of ovules	Anatropous, hemianatropous	Anatropous
Placentation	Axile, basal, or infrequently parietal	Axile, rarely parietal
SEEDS		
Microphyle	Formed of outer integument	Formed of both integuments
Testa:		
No. of integuments	Bitegmic	Bitegmic
Outer integument	2–30 cells thick	2 cells thick
Inner integument	2–15 cells thick	2–6 cells thick
Nucellus	Tenuinucellate	Tenuinucellate
Endosperm	Nuclear	Nuclear
Embryogeny	Solanad type	Onagrad type

families represented in the Cretaceous floras, as well as 62% of extant dicotyledons, have two distinct integuments producing the seed coat (Sporne 1974). A sarcostesta (Corner 1953) is considered more primitive (van der Pijl 1955) than a sclerotesta as in *Sahniocarpon*. Sporne (1974) noted that the septa in axile placentation is a single unit formed by fusion of individual, involute carpels.

Members of both Guttiferae and Lecythidaceae are present in the fossil floras of India. Jain (1964) and Nambudiri (1969) described species of dicotyledonous fruit resembling Guttiferae. *Indocarpa* and the *Sahniocarpon* specimens were collected from the same Intertrappean locality at Mahgaon Kalan. Lakhanpal and Bose (1951) described leaves of *Garcenia* and *Calophyllum* (Guttiferae) from the Tertiary beds in Rajastan. Wood genera such as *Kayeoxylon assamicum* (Chowdhury and Tandon 1949) and *Guttiferoxylon indicum* (Ramanujam 1960) also occur in the Tertiary beds of India. Shallom (1960) reported *Barringtonioxylon deccanense*, a fossil wood assignable to Lecythidaceae, from the Deccan Intertrappean beds of India.

On comparison with extant genera, the *Sahniocarpon* fruit is found to resemble fruits of members of the families Clusiaceae (Guttiferae *sensu stricto;* Cronquist 1968, 1981, Takhtajan 1969) and Lecythidaceae. Taxonomists have treated Clusiaceae and Hyperiaceae as separate families or subfamilies under Clusiaceae. We have adopted Cronquist's (1981) system in which subfamilies Clusioideae and Hypericoideae have been included under the family Clusiaceae. The subfamily Clusioideae has capsular fruits, as in *Sahniocarpon*, with 3–5 carpels forming the fruit. These subfamilies have 1–numerous seeds attached to the base of the axile placentum. Moreover, the seeds are bitegmic. The difference between *Sahniocarpon* and the several genera of Clusioideae is that micropyles in seeds of the modern genera of this subfamily are formed entirely of their outer integuments (Table 1, Davis 1966). *Sahniocarpon* differs from Hypericoideae as well, the major difference between them being the number of seeds in each locule of the fruit. In Lecythidaceae, the ovules are anatropous. They are bitegmic but the micropyle is formed only of the inner integument (Venkateswarulu 1952). Although the genera of Clusiaceae are not similar to *Sahniocarpon* in all aspects, the resemblances between the extant genera of this family and *Sahniocarpon* are close enough to tentatively assign this genus to the Clusioideae of the tropical family Clusiaceae.

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MATERNAL CARE OF NEONATES IN THE PRAIRIE SKINK, *EUMECES SEPTENTRIONALIS*

Louis A. Somma[1]

ABSTRACT.—Maternal care of neonates has been documented in relatively few species of lizards representing four families. This study documents the occurrence of maternal care of neonates in the prairie skink, *Eumeces septentrionalis*. Observations made herein indicate that individual variation in maternal behavior exists in this species.

Maternal care of neonates has been documented in relatively few species of lizards. Parental protection of neonates and assistance during parturition or hatching, however, does occur in some lizard species in the families Gekkonidae (Robb 1986), Anguidae (Guillette and Hotton 1986), Scincidae (Tanner 1943, 1957, Evans 1959, Rose 1962, Hikida 1981, Slavens 1983, Hammond 1985, Mehaffey 1986), and Xantusidae (Cowles 1944). Initial observations on maternal care in *Eumeces septentrionalis* have been made by Somma (1985). The observations presented herein represent a more detailed description of maternal care of neonates by *E. septentrionalis*.

Five gravid females were obtained from Douglas County, Nebraska, during May 1984 and placed in separate plastic terraria with a soil substrate. A 14L:10D photoperiod was maintained for the duration of the study. Each terrarium contained a 15 × 15-cm plate of transparent, red acrylic under which the skinks could brood their eggs and be observed. Lizards were fed mealworms and crickets ad libitum. Eggs were oviposited between 18 and 30 June and brooded until hatchling emergence (14–23 July).

The type of maternal behavior expressed toward neonates was highly variable, although no attempt was made to quantify it. One female did not express any behavior toward its single surviving hatchling. Two females nudged their young while they emerged and then groomed them by licking the embryonic fluids from their bodies. These and two others each constructed small burrows extending 5–7 cm from their nest cavities during hatchling emergence. Most of the neonates remained in these burrows with the adults for two days. All four adults followed their young around the nests while constantly directing tongue-flicks toward them. One female remained tightly coiled around its neonates at all times. These maternal behaviors lasted for two days before the adult skinks ignored their neonates and left their nests. At this time, both adults and neonates made attempts to escape their respective terraria.

The maternal behaviors of the skinks observed in this study were not as pronounced as those reported earlier for this species (Somma 1985). In that study, the females remained with the hatchlings for three days and attempted aggressively to defend their young. The results of past and present observations on maternal behavior in *Eumeces septentrionalis* indicate that much variation exists. Further studies are required to evaluate the significance of this behavior.

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THERMAL TOLERANCES AND PREFERENCES OF FISHES OF THE VIRGIN RIVER SYSTEM (UTAH, ARIZONA, NEVADA)

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ABSTRACT.—Critical thermal maxima (CTM) and thermal preferenda of the common fishes of the Virgin River were examined. Differences in final temperature preferenda and CTM for species with low thermal lability (speckled dace, spinedace, roundtail chub) correspond well with differences in their distribution and abundance in the river. These species shifted their acute thermal preferences relatively little as acclimation temperature increased. For thermally labile species (woundfin, red shiner, desert sucker, and flannelmouth sucker), the final preferendum is a less precise indicator of probable distribution. The woundfin, an endangered fish, has a high CTM (39.5 C at 25 C acclimation) and a labile acute preferendum (slope nearest 1) compared to other species in the system. The introduced red shiner likewise has a high CTM and a labile acute preferendum. In cooler temperatures, its acute preferendum shifts more rapidly than does that of the woundfin. At higher temperatures (above 15 C), the red shiner does not shift its acute preferendum as rapidly as does the woundfin. The red shiner, however, has a higher final preferendum. For thermally labile species, influence of acclimation temperature on mean preferendum, together with CTM, provides a better insight into distributional relationships within the system.

In recent years, agricultural, municipal, and industrial water uses in arid regions of the southwestern United States have reduced both stream flows and water quality. The consequent alterations in thermal, chemical, and flow regimes, coupled with the discharge of various effluents and the introduction of nonnative fishes, have seriously reduced many native fish stocks (Deacon and Minckley 1974, Deacon 1979, Pister 1979, 1981).

The Virgin River in Utah, Arizona, and Nevada is an example of such a system. Its shifting, sandy bottoms, steep gradients, high sediment loads, variable flows, large daily and seasonal fluctuations in temperature, and other physical and chemical characteristics are typical of desert streams (Cook 1960, Deacon and Minckley 1974, Naiman 1981). Below Zion National Park, Utah, several natural physicochemical and geographic barriers disrupt the continuity of the biotic communities. These include Pah Tempe Springs, a series of over 100 saline hot springs emerging along the Hurricane Fault in Utah; and the Virgin River Gorge in Arizona where, during much of the year, the entire flow seeps below ground and reemerges in springs above Littlefield, Arizona (Sandberg and Sultz 1982).

The fish fauna of the Virgin River consists of only six native species: speckled dace (*Rhinichthys osculus*); flannelmouth sucker (*Catostomus latipinnis*); desert sucker (*Catostomus [Pantosteus] clarki*); Virgin spinedace (*Lepidomeda mollispinis mollispinis*) and Virgin roundtail chub (*Gila robusta seminuda*), the latter two of which are endemic subspecies; and woundfin (*Plagopterus argentissimus*), which is an endemic species. The woundfin is listed as endangered (U.S. Fish and Wildlife Service 1986), the Virgin roundtail has been recommended for endangered status, and the Virgin spinedace has been recommended for threatened status (Deacon 1979, Deacon et al. 1979). The red shiner, *Notropis lutrensis*, was introduced into the Colorado River system as a bait fish in the early 1950s (Hubbs 1954). Of the 13 introduced fish species recorded from the lower Virgin River (Cross 1985), only the red shiner has become well established (Williams 1977, Cross 1978a).

Agricultural diversion and groundwater use since 1900 have reduced flows in the mainstream to the extent that long stretches may be dry during summer months. Following completion of the Quail Creek Reservoir project early in 1985, an unanticipated, dramatic increase in discharge of Pah Tempe Springs

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caused increases in both temperature and salinity throughout the downstream segment of the Virgin River in Utah (Deacon, in press). Summer river temperatures fluctuate by 15–20 C daily, reaching 36 C in some areas (Cross 1975, Deacon 1977, Schumann 1978). However, except for the roundtail (Schumann 1978) and Virgin spinedace (Espinosa and Deacon 1978), the temperature responses of the native fishes have not been examined.

This paper reports preliminary investigations of the temperature tolerances and preferences of the native fishes and the introduced red shiner.

Methods and Materials

Collection and Maintenance of Specimens

Suckers, spinedace, speckled dace, woundfin, and red shiners were collected during May and June using 10-m nylon seines with 6.4-mm mesh. Virgin roundtail adults were collected between April and October. Captured fish were acclimated in aerated and filtered 450-liter and 1100-liter aquaria, containing aged tap water maintained at temperatures of 10, 15, and 25 ± 1 C, for at least two weeks before testing (Otto 1973, Feldmeth and Baskin 1976, Otto and Rice 1977). Fish were maintained on a 12-hour photoperiod and fed Purina Trout Chow daily. Food was withheld for 25 hours prior to experimentation. All experiments were conducted between June and August to avoid the influences of seasonality and aging (McCauley et al. 1977).

Critical Thermal Limits

Tolerance of high temperature was measured as critical thermal maximum (CTM) (Lowe and Heath 1969, Fry 1971, Feldmeth and Baskin 1976). The CTM was determined for six individuals of each species at each acclimation temperature in an aerated 13-liter glass chamber immersed in a Masterline 2095 water bath. Fish were introduced into the chamber at their acclimation temperature. After a 60-minute adjustment period, the chamber was heated at a constant rate of 0.24 C/minute until the animal lost equilibrium. At that point the fish was immediately returned to its acclimation temperature. No more than three fish were used in a single test. The temperature at which loss of equilibrium is observed is an unambiguous endpoint, ecologically equivalent to death in a natural situation where the animal would then be unable to escape lethal conditions (Fry 1971). CTMs were not measured for 15-C–acclimated suckers of either species (see next section).

Thermal Preferendum

Acute preferred temperatures (Reynolds and Casterlin 1979) were determined for six individuals of each species (except the suckers and the roundtail chub) at all acclimation temperatures. Testing was done in a horizontal gradient consisting of three 20-liter aquaria joined lengthwise and partitioned to give six small chambers, each 16 × 20 × 21 cm. One end was cooled by plastic-coated copper coils through which refrigerated water was circulated, while the other end was heated with 100-W aquarium heaters. Aeration in each cell prevented gas supersaturation and temperature stratification. Fish could thus choose temperatures between approximately 8 C and 35 C. Tests were observed from behind a blind, and temperatures were measured by mercury thermometers in each chamber.

Preliminary tests without a thermal gradient demonstrated that selection was not spatially influenced in any of the species. This was further avoided during the course of the experiments by a slight shift of temperatures along the gradient.

Two or three individuals of a single species were introduced into the chamber closest to their acclimation temperature and left undisturbed for 30 minutes. Chamber temperatures and the distribution of the animals in the gradient were then recorded at 10-minute intervals for one hour, and at 20-minute intervals for the next two hours. The fish were then removed and their length and weight recorded (Table 1).

Time and resource constraints prevented our collecting enough suckers (of either species) to provide complete acclimation groups. Therefore, preferenda are reported for fewer than six individuals at most acclimation temperatures (Table 2). Likewise, insufficient numbers of Virgin roundtail adults small enough to fit the apparatus were available at the time of the tests. Consequently, young-of-the-year roundtails spawned in captivity from adults captured from the nearby Moapa River in Nevada were acclimated to 8 C, 22 C, 25 C,

TABLE 1. Critical thermal maxima (CTM) at three acclimation temperatures for the common fishes of the Virgin River. Each number is the mean ± 1 standard deviation for six fish, except that only three desert suckers were used at 25 C and three flannelmouth at 10 C. A range in length is shown for roundtail.

Species	T_{accl} (°C)				
	10	15	25	Length (mm)	Weight (gr.)
Roundtail chub	27.90 ± 0.22	32.30 ± 1.39	36.41 ± 0.66	120 – 233	62.60 ± 47.60
Speckled dace	30.47 ± 1.60	32.57 ± 0.46	36.82 ± 0.63	72.17 ± 12.70	3.73 ± 1.86
Virgin spinedace	30.25 ± 0.40	32.90 ± 0.30	37.02 ± 0.44	95.79 ± 7.66	8.54 ± 1.99
Woundfin	30.70 ± 0.21	33.58 ± 1.01	39.47 ± 0.21	71.27 ± 10.56	3.35 ± 1.35
Red shiner	30.10 ± 1.05	33.07 ± 0.59	38.80 ± 0.71	61.47 ± 6.43	2.92 ± 1.06
Desert sucker	32.30 ± 0.64	—	37.17 ± 0.50	124.60 ± 22.89	16.35 ± 7.33
Flannelmouth sucker	31.22 ± 1.08	—	36.98 ± 0.29	155.60 ± 20.94	27.57 ± 9.48

TABLE 2. Distribution of native and introduced fishes of Virgin River in a thermal gradient. Fish were acclimated to 10, 15, and 25 C. Data for the Virgin roundtail are in Schumann (1978).

Species				Temperature				
	Accl. temp.	# fish	# obs.	Max.	Min.	Mean	σ	Mode
Speckled dace	10	6	77	20	10	14	4.4	9.5 – 10.5
	15	6	78	26	14	16	2.8	14 – 15
	25	6	71	27	9	16	4.2	15 – 16
Virgin spinedace	10	6	68	26	10	19	3.8	18.5 – 19.5
	15	7	86	31	15	21	3.7	21.5 – 22.5
	25	6	78	29	15	23	3.4	24 – 25
Woundfin	10	6	78	20	10	11	2.3	10 – 11
	15	6	69	23	14	16	3.6	14 – 15
	25	6	72	32	13	24	4.8	23.5 – 24.5
Red shiner	10	6	78	22	10	12	3.8	10 – 11
	15	6	50	31	15	23	4.9	23 – 24
	25	6	75	34	10	27	5.0	30 – 31
Desert sucker	10	6	80	28	10	13	4.3	10 – 11
	25	3	36	30	10	22	3.5	20 – 21
Flannelmouth sucker	10	3	46	25	10	14	5.0	10 – 11
	25	6	65	34	15	26	2.8	26 – 27

and 30 C and tested in the same manner as the other species (Schumann 1978). As with the 15-C–acclimated suckers, results were not compared statistically with the other fish but are presented here to complete the picture for the native species.

Analysis of Data

CTM data were analyzed by Welch's unequal-variance analysis of variance (ANOVA) and Bonferroni paired comparisons. Regression lines for CTMs were constructed and compared by covariance analysis (Dixon 1981).

Significance of temperature selection was verified by chi-square tests for each species. Differences between species and between acclimation temperatures were tested by Welch's unequal-variance ANOVA and Bonferroni paired comparisons (Dixon 1981). These were verified by two-way ANOVA (Burr 1974) and two-way Friedman's test (Tate and Clelland 1957) of the means for each group. Nonlinearity of preference curves was verified by regression analysis (Dixon 1981).

RESULTS

Temperature Tolerance

CTM increased in a linear fashion with acclimation temperature for all species examined. Within any given species, mean CTM values differed significantly ($p < .05$) at different acclimation temperatures (Table 1). CTMs were not significantly different ($p > .05$) between species in either the 10-C– or

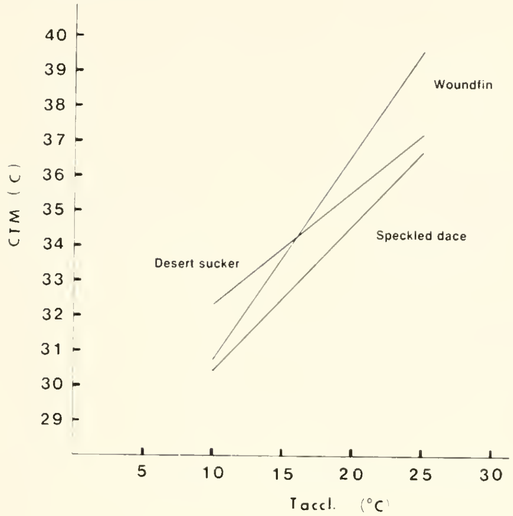

Fig. 1. The effect of acclimation temperature on critical thermal maximum in three Virgin River fishes. Regression lines are presented for one representative species of each group described in the text.

15-C–acclimation groups. However, at 25 C acclimation, the mean CTMs of woundfin and red shiner each differed significantly from all other species ($p < .05$), although they were not significantly different from each other ($p > .05$).

The lines relating CTM to acclimation temperature have slopes ranging from 0.28 (desert sucker) to 0.59 (woundfin). These are illustrated in Figure 1 along with that of the speckled dace, which is intermediate at 0.42. The flannelmouth sucker (0.38), Virgin spinedace (0.45), Virgin roundtail (0.48), and red shiner (0.58) also fall between the extremes. An increase in slope indicates that acclimation temperature has an increased effect on CTM.

Thermal Preference

The frequency distribution of each species in the thermal gradient (Table 2) suggests that variation and skewness were associated with some experimental groups (Richards et al. 1977). For any given species, the mean acute preferred temperature observed at one acclimation temperature differed significantly at the .05 level from the mean preferendum at any other acclimation temperature, with one exception: no significant difference ($p > .05$) was found between acute preferenda of 15-C– and 25-C–acclimated speckled dace. In all other cases, an increase in acclimation temperature shifted thermal preferenda upward (Figs. 2 and 3). Mean acute preferenda equaled or exceeded acclimation temperature for all species acclimated to 10 C and 15 C. At 25 C acclimation, however, this was true only for the flannelmouth sucker and the red shiner. Modal preferred temperatures likewise equaled or exceeded temperature of acclimation for all species acclimated to 10 C and for all species except woundfin at the 15-C–acclimation level. As was found for the means, modal preferenda in the 25-C–acclimation group were greater than or equal to acclimation temperature for only flannelmouth suckers and red shiners.

DISCUSSION

Despite the large body of information on the physiological performance of organisms with respect to temperature, surprisingly few studies relate this clearly to the organism's ecology (Ferguson 1958, Gift 1977, Richards and Ibara 1978, Huey and Stevenson 1979, Beitinger and Fitzpatrick 1979, Calhoun et al. 1982, Matthews 1986). Only recently have formalized attempts been made to define a "thermal niche" for ectotherms and to apply concepts of niche theory and competition to the thermal resource (Fry 1971, Alderdice 1972, Hutchinson 1978, Magnuson et al. 1979). The Virgin River's considerable spatial and temporal variation in water temperature places greater value on eurythermal species that can operate as "thermal generalists" under suboptimal conditions, but respond opportunistically when preferred thermal situations are encountered. This is the established pattern for desert spring and stream fishes for such factors as food and space (Deacon and Minckley 1974).

Magnuson et al. 1979 state that lethal temperatures are so extreme as to say little about the "fine tuning" of an organism's utilization of its thermal resource. However, these set the outermost limits of the thermal niche and form the bounds of the thermal resistance zone (Reynolds and Casterlin 1979). Our CTM values (Table 1) illustrate the eurythermality of these desert species. This is shown further by the ranges associated with the acute thermal preferences (Table 2). We recorded observations between 10 C and

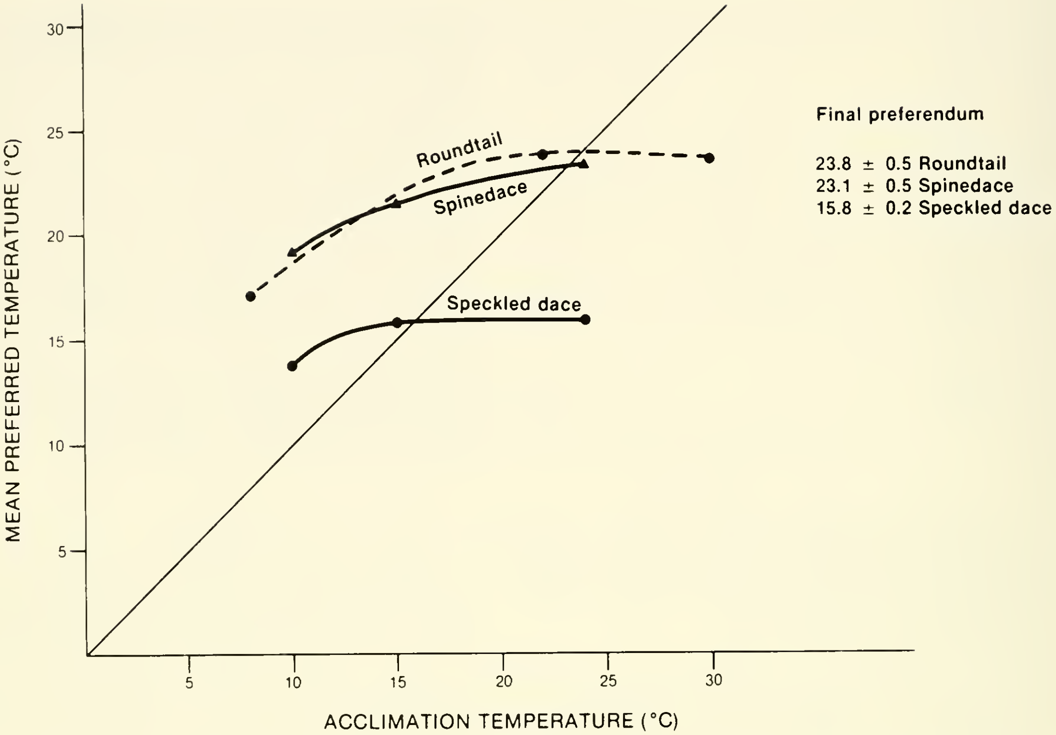

Fig. 2. Influence of acclimation temperature on mean preferred temperature in Virgin River fishes of low thermal lability. Lines fitted by eye.

32–34 C for all species except the desert sucker and speckled dace. Further, when Magnuson et al.'s (1979) operational definition of thermal niche breadth (i.e., mean preferred temperature ± one standard deviation) is applied to Figure 2, all species exhibit ranges 5–10 C in breadth at all acclimation temperatures. This implies that desert fishes tend to have broader thermal niches than most temperate freshwater fishes previously considered (Reutter and Herdendorf 1974, Beitinger et al. 1975, Coutant 1977, Magnuson et al. 1979).

Nearly all species tested exhibited skewed preferred temperature distributions (Table 2). This resulted in differences between the various measurements of central tendency used to describe them. The skewed patterns may be partly attributable to the design of the apparatus, but similar findings have been reported by De Witt (1967), Reynolds and Casterlin (1976, 1979), and others using a variety of designs. This widespread phenomenon and its possible causes and effects have been reviewed in detail by De Witt and Friedman (1979).

Fry (1947) defined the final thermal preferendum, in part, as being the point where preferred temperature equals acclimation temperature. He considered this a largely species-specific phenomenon, independent of the animal's previous thermal history. This concept has garnered considerable attention in recent years, although, surprisingly, its potential for bridging the gap between thermal physiology and ecology has remained relatively unexplored (Reynolds 1977).

The results of our attempts to define the final thermal preferendum of the Virgin River fishes are shown in Figures 2 and 3. Each curve was fitted by eye to the mean acute preferendum values according to the method of Reynolds and Casterlin (1979) (see also Otto and Rice 1977, Garside et al. 1977, Richards and Ibara 1978). This gave approximate final preferenda of 27.0 C for the red shiner, 25.9 C for the flannelmouth sucker, 23.8 C for the roundtail, 23.1 C for the spinedace, 19.5 C for

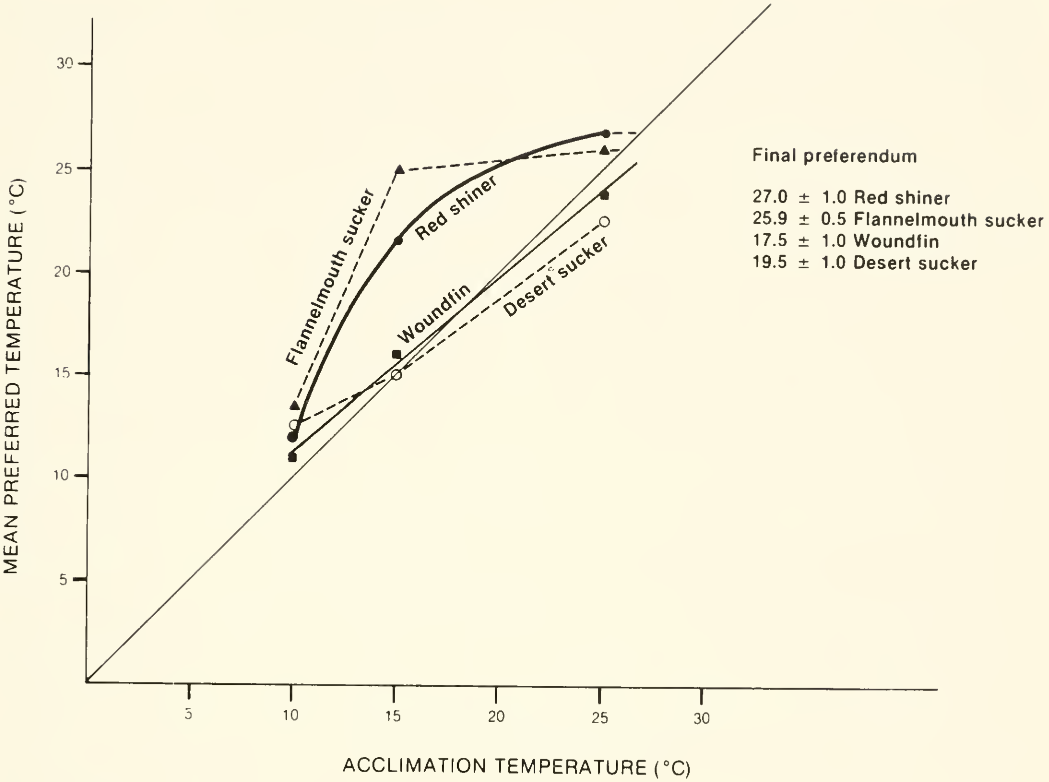

Fig. 3. Influence of acclimation temperature on mean preferred temperature in thermally labile Virgin River fishes. Dashed curves are hypothesized from responses of a single 15-C–acclimated specimen (see text). Lines fitted by eye.

the woundfin, 17.5 C for the desert sucker, and 15.8 C for the speckled dace. Final preferenda of 30.0 and 23.3 C have been determined for populations of red shiner in two distinctly different habitats in Texas (Calhoun et al. 1982).

Three types of curves are represented in Figures 2 and 3. The curves most closely approximating the line of equality (Fig. 3) indicate a maximally thermally labile species. This situation, represented most strongly by the woundfin, suggests that the species prefers the temperature in which it finds itself. This may be adaptive for a fish subjected to widely varying thermal conditions. As long as it can acclimatize successfully to ambient conditions, it probably operates near peak physiological efficiency throughout much of the range of seasonal variation encountered (Beitinger and Fitzpatrick 1979). The curves diverging most strongly from the line of equality (Fig. 2) characterize species whose preferred temperature remains nearly unchanged despite wide variations in acclimation temperature (Brett 1952, McCauley et al. 1977). The curves for the red shiner and flannelmouth sucker (Fig. 3) differ from both of the above two types. At cooler temperatures, rising acclimation temperatures shift preferenda upward rapidly, while at warmer temperatures, acclimation temperature has relatively little influence on preferred temperature. These three apparently different types of curves provide interesting insight into the ecology and distribution of fishes in the Virgin River.

The woundfin has a high CTM, relatively low final preferendum, and the most labile acute preferendum of any of the species examined. It is the dominant native species in the moderately altered sections of the middle and lower mainstream where temperature variability is extreme (Cross 1978a, Deacon and Hardy 1984). The thermal lability of the woundfin is most strikingly demonstrated by the ability of acclimation temperature to influence preferred temperature. This capability, however, becomes somewhat reduced at higher temperatures as the thermal selection curve diverges from the line of equality (Fig. 3). At higher temperatures, then, the red shiner may have an advantage over woundfin, while at lower temperatures (below 25 C), the reverse may occur.

The thermal selection curve for the desert sucker suggests that it, too, is thermally labile. It diverges more from the line of equality at both higher and lower temperatures than does the woundfin; however, the final preferendum is also somewhat lower, suggesting a more upstream (cooler) pattern of distribution and abundance than woundfin. The desert sucker is in fact the most widely distributed species in the Virgin River system, reaching greatest abundance in middle and lower tributaries and the upper mainstream. Abundance drops in the lower, warmer mainstream and in the upper, cooler tributaries (Cross 1975, 1985).

The thermal selection curves of the other native species are uniformly similar in shape, differing primarily in vertical displacement. All appear less labile than the woundfin and desert sucker. The speckled dace, with the lowest final preferendum, has the most upstream distribution. It achieves greatest abundance in middle and lower tributaries and the upper mainstream. In the middle and lower mainstream it is almost always associated with cool, clear inflowing tributaries or springs. The Virgin spinedace, with the next highest final preferendum, has a slightly more downstream distribution. It is most abundant in lower tributaries and the upper mainstream. More downstream occurrences are primarily associated with tributary and spring inflows. The flannelmouth sucker has the highest final preferendum, but reaches its greatest abundance in the upper mainstream. Its downstream distribution, however, is not as restricted to tributary and spring inflow as are those of the speckled dace and spinedace. In general, the distributional relationships of these three species (Cross 1975) correspond well with the thermal relationships illustrated in Figures 2 and 3. Note also that the flannelmouth sucker (which had the highest final preferendum of any native species) and the woundfin (with the highest CTM) most often approach the Pah Tempe hot spring inflows more closely than other species (Cross 1975, Williams 1977).

The Virgin roundtail has a thermal selection curve very similar to that of the spinedace. It has the lowest CTM value of any native species in the river and an intermediate final preferendum. Acclimation temperature has relatively little influence on its preferred temperature. This species is confined to the middle and lower mainstream of the Virgin River below Pah Tempe Springs (Cross 1978b). The roundtail is no longer perennially abundant anywhere within its range, although there is evidence that it once was (Cross 1978b). Increased diversion of water for irrigation, increased irrigation return flow in the heat of the summer, clearing of streamside vegetation, overgrazing in the watershed, and other activities associated with man's use of the region may have increased summer temperatures within the range of the roundtail. Lack of suitable tributary streams, plus the barrier provided by Pah Tempe Springs, has perhaps prevented upstream displacement of roundtail populations. Their thermal relationships suggest a pattern of distribution and abundance in the Virgin River similar to that of the spinedace. The fact that most good spinedace habitat is unavailable to the roundtail may partly explain its present precarious status in the Virgin River.

The thermal selection curves for the red shiner and flannelmouth sucker are different from those of other native species. The red shiner has a high CTM, and a higher final preferendum than any native species. It occurs throughout the lower mainstream but, until 1985, was abundant only in the deeper water (> 8 cm) of the highly modified lower reach, where the flow is intermittent through a wide, shallow, braided channel. Here, summer temperatures appear to exceed 30 C more often, and for longer periods, than elsewhere in the river. The red shiner is the dominant species in this segment of the river and is often accompanied by fewer numbers of woundfin. Other native species occur sporadically. Occasionally woundfin reach numbers nearly equaling those of the red shiner (Cross 1975, Deacon and Hardy 1984, Deacon, in press).

Woundfin and red shiner shift their CTM

more markedly in response to increase in acclimation temperature than do other species. This apparently provides both species with an advantage over other native fishes in the warmer, more thermally variable, shallow waters of the lower river. The higher final preferendum exhibited by the red shiner suggests that that species may have a thermal advantage over the woundfin during the summer in this lower segment of the mainstream.

The flannelmouth sucker has only a slightly lower final preferendum than does the red shiner, but at an acclimation temperature of 25 C the sucker has a significantly lower CTM. This may partly explain the near absence of the flannelmouth sucker in Virgin River below Mesquite, Nevada.

Thermal tolerance and preference relationships are not the only factors involved in niche partitioning in the Virgin River. Preferred temperatures may be unavailable over large stretches of the river, or for long periods of time. Interactions influencing utilization of food, space, and other resources affect the fishes as well (Cross 1975, 1978a, 1978b, Deacon 1979, Deacon and Hardy 1983, Greger 1983). Temperature relations determined in the laboratory do not always correspond well to field distributions (Reynolds 1977, Magnuson et al. 1979, Reynolds and Casterlin 1979), but in the case of the Virgin River fishes, the correspondence is striking.

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SIX NEW SCOLYTIDAE (COLEOPTERA) FROM MEXICO

Stephen L. Wood[1]

Abstract.—*Alniphagus africanus* Schedl, 1963, and *Hylesinus africanus* Schedl, 1965, were both transferred to *Hylesinopsis* and thereby become junior homonyms of *H. africanus* (Eggers, 1933). The new name *H. acacicolens* is proposed as a replacement for Schedl's 1963 name and *H. secutus* as a new name for Schedl's 1965 name. Six species from Mexico are described as new to science, including: *Hylocurus atkinsoni*, *H. crotonis*, *Monarthrum xalapensis*, *Pseudochramesus jaliscoensis*, *Pseudopityophthorus durangoensis*, and *P. xalapae*.

On the following pages two junior homonyms are renamed in the African genus *Hylesinopsis*, and six species new to science are described from Mexico. The new species represent the genera *Hylocurus* (2), *Monarthrum* (1), *Pseudochramesus* (1), and *Pseudopityophthorus* (2). This is the first record of the genus *Pseudochramesus* north of Bolivia and Brazil.

Hylesinopsis acacicolens, n. n.

Alniphagus africanus Schedl, 1963, Ent. Abh. Mus. Tierk. Dresden 28:259 (Holotype, sex?; Riff Valley, Kenya; Wien Nat. Mus.)

The species named by Schedl (1963:259) as *Aniphagus africanus* is here transferred to the genus *Hylesinopsis*. This transfer makes it a junior homonym of *H. africanus* (Eggers 1933:19) that was originally named in *Pseudophloeotribus*, transferred to *Metahylesinus* by Schedl (1957:9), then to *Hylesinopsis* (Wood 1986:39). The new name *acaciocolens* is proposed as a replacement for *africanus* Schedl 1963.

The genus *Alniphagus* occurs only on the northern Pacific Coast from Japan to California and is quite unrelated to the African fauna.

Hylesinopsis secutus, n. n.

Hylesinus africanus Schedl, 1965, Novos Taxa Ent. 38:4 (Holotype, female; Uganda, Mpanga; British Museum [Natural History]).

The species named as *Hylesinus africanus* Schedl (1965:4) is here transferred to *Hylesinopsis*. This transfer makes it a junior homonym of *H. africanus* (Eggers 1933:19) that was originally named in *Pseudophloeotribus* before it was transferred to *Hylesinopsis* (Wood 1986:39). The new name *secutus* is proposed as a replacement for *africanus* Schedl 1965.

The genus *Hylesinus* is not known to occur in Africa south of the Sahara Desert.

Hylocurus atkinsoni, n. sp.

This species is distinguishesd from the closely allied *prolatus* Wood by the much smaller size, and by the more conservative sculpture of frons and elytral declivity of both sexes as described below.

Male.—Length 1.7 mm (paratypes 1.8–2.1 mm), 2.8 times as long as wide; color very dark brown.

Frons similar to *prolatus*, modestly, transversely impressed below level of antennal insertion, moderately elevated above into an indefinite, transverse, subcarinate elevation; surface rather coarsely reticulate-granulate, with rather coarse, moderately close tubercles above; vestiture sparse, inconspicuous; antenna about as in *prolatus*.

Pronotum outline as in *prolatus;* deeply reticulate on posterior half, a few small crenulations on median area to base. Vestiture evident only at margins.

Elytra less slender and apex more obtusely pointed than in *prolatus;* strial punctures slightly smaller, not as deep, interstriae smooth and impunctate except near declivity. Declivity not as abrupt or as steep as *prolatus;* sculpture resembling *prolatus* except tubercles on 1 and 3 continued to level of junction of 5 and 7, 4, 5, 6, and 7 with tubercles continuing to their apices; 9 elevated but less abrupt than in *prolatus;* apex strongly mucronate.

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Vestiture restricted to interstriae at base of declivity, equal in abundance to *prolatus*, but much stouter, about half as long.

FEMALE.—Similar to male except frons with impression and elevation largely obsolete, sculpture much finer, tubercles mostly obsolete, upper frons with a very few setae in median area (resembling *prolatus* but much less abundant); sculpture of pronotum and elytra much finer, declivity more evenly convex, tubercles much smaller, less conspicuous; declivital setae more slender.

TYPE LOCALITY.—El Casillo, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and two broken paratypes were taken at the type locality on 18-VII-1983, No. 9, *Inga* sp., by Felipe A. Noguera. One paratype bears the same locality and date, No. 3-917, *Acacia pennatula*, Atkinson and Equihua. Four paratypes are from Banderilla, Veracruz, Mexico, 24 Nov. 1983, No. 96, *Leucaena pulverulenta*, Felipe A. Noguera.

The holotype, allotype, and paratypes are in my collection.

Hylocurus crotonis, sp. n.

This species is distinguished from the allied *incomptus* Wood and *nodulus* Wood by the smaller size, much stouter male declivital setae, and by other characters described below.

MALE.—Length 1.8 mm (male paratype 1.8 mm), 2.6 times as long as wide; color black.

Frons resembling *incomptus* except transverse carina longer, more definite, length more than two-thirds distance between eyes; surface finely rugose reticulate, granules and punctures not clearly evident; vestiture short, sparse, inconspicuous.

Pronotum similar to *incomptus* except anterior margin armed by a row of six rather coarse serrations; posterior half more strongly rugose reticulate, tubercles closer, more sharply defined; setae coarser.

Elytra about as in *incomptus* except strial and interstrial punctures more clearly impressed, those of interstriae almost as large as those of striae, becoming somewhat tuberculate near declivity; declivital sculpture similar except transverse impression on lower half not as strong, all tubercles smaller; vestiture largely confined to declivital interstriae, longest equal in length to distance between rows, each very stout, about 8 times as long as wide, shorter on lower declivity toward suture.

TYPE LOCALITY.—Estacion de Biologia, Chamela, Jalisco, Mexico.

TYPE MATERIAL.—The male holotype and one male paratype were taken at the type locality 10-X-1982, 100 m, S-817, from *Croton pseudoniveus*, by T. H. Atkinson and A. Equihua.

The holotype and paratype are in my collection.

Monarthrum xalapensis, n. sp.

This species superficially resembles the *scutellare* portion of this genus, but its true affinities lie with species allied to *dimidiatum* Ferrari. From *dimidiatum* it is distinguished by the conspicuously different elytra in both sexes, and by other minor details described below.

MALE.—Length 2.0 mm (paratypes 1.9–2.0 mm), 3.2 times as long as wide; color reddish brown.

Frons broadly, evenly convex; surface finely reticulate, upper and lateral areas with shallow, rather small punctures except obsolete on median half of lower half, this area appearing spongy but without any indication of microsetae. Antennal club subcircular, with two moderately procurved sutures marked by setae; funicle 2–segmented.

Pronotum about as in *dimidiatum*.

Elytral outline resembling *dimidiatum* except not tapered toward apex, disc more strongly reticulate, declivity more broadly, deeply excavated, sutural emargination equal. Lateral margin of declivity from base to emargination strongly, acutely elevated (considerably more so than in *dimidiatum*); margin armed on upper fourth by a coarse, pointed denticle in position of striae 3, a second obtuse denticle of almost equal size directed somewhat mesad on lower third; no other irregularities on margin; floor of excavated area shining, weakly reticulate, with small, confused, moderately abundant punctures. Glabrous except for sparse setae on sides near declivity. Protibiae armed more coarsely than in *dimidiatum* on same pattern.

FEMALE.—Similar to male except frons punctured throughout, epistoma armed on margin by a small tubercle; declivity resembling female *dimidiatum* except lower area less broadly impressed, upper denticle similar, lower denticle obtuse, submammiform, displaced mesad (as close as upper pair).

Type locality.—Jalapa, Veracruz, Mexico.

Type material.—The male holotype, female allotype, and six paratypes were taken at the type locality on 8-IX-1983, No. 53, by Filipe A. Noguera.

The holotype, allotype, and paratypes are in my collection.

Pseudochramesus jaliscoensis, n. sp.

This is the first record of *Pseudochramesus* north of Bolivia and Brazil. This species is allied to *opacus* Schedl, but is distinguished by the smaller size, by the less distinctly tuberculate anterolateral areas of the pronotum, and by the very different male frons.

Male.—Length 1.4 mm (paratypes 1.4–1.5 mm), 1.4 times as long as wide; color black, some setae pale.

Frons with antennal insertion near middle of longitudinal axis, their bases separated by half distance between eyes about as in *opacus;* median area less strongly sulcate than in *opacus*, slightly narrower, not as smooth, fine tubercles clearly evident particularly laterally and above, scrobelike impressions not as deep or as extensive; transverse epistomal elevation not as high or as distinct as in *opacus*. Antenna about as in *opacus*.

Pronotum similar to *opacus*, punctures smaller, much less distinct, tubercles on anterior half and lateral areas distinctly larger, more numerous.

Elytra similar to *opacus*, striae apparently less strongly impressed and less strongly punctured, and crenulations on elytral bases appear narrower.

Female.—Similar to male except frons broadly convex, antennal bases separated by same distance as eyes, fine tubercles present as in male.

Type locality.—Carretera Barra Navidad–Puerto Vallarta, Jalisco, Mexico.

Type material.—The male holotype, female allotype, and eight paratypes were taken at the type locality on 21-X-1985, No. 360, from *Cynometra oaxacana*, by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Pseudopityophthorus durangoensis, n. sp.

This species is distinguished from *tenuis* Wood by the larger size, by the longer setae on the ventrolateral areas of the declivity, and by details of frontal sculpture and ornamentation in both sexes.

Male.—Length 1.5 mm (paratypes 1.4–1.7 mm), 3.0 times as long as wide; mature color dark brown.

Frons more broadly, more strongly impressed than in *tenuis*, setae slightly longer.

Pronotum appearing more elongate than in *tenuis* and with punctures on posterior half more numerous and larger.

Elytra as in *tenuis* except strial punctures more definite, both strial and interstrial setae distinctly longer, strial punctures on declivity minute, but more clearly identifiable.

Female.—Similar to male except frons resembling female *tenuis* but less strongly impressed below, more strongly above, upper half coarsely irregular, almost aciculate, lower half with a rather strong median carina extending almost to epistomal margin, setae longer, much more conspicuous.

Type locality.—Ninety-six km (60 miles) west of Durango, Durango, Mexico.

Type material.—The male holotype, female allotype, and 32 paratypes were taken 5-VI-1965, 2,300 m (7,000 ft), No. 30, from *Quercus*, by me. Three paratypes are labeled 3 miles W El Salto, Durango, Mexico, 7-VI-1965, 7,500 ft, No. 41, *Quercus*, taken by me. One paratype is from 10 miles W El Salto, Durango, Mexico, July 1964, J. B. Thomas.

The holotype, allotype, and paratypes are in my collection.

Pseudopityophthorus xalapae, n. sp.

This species is distinguished from *durangoensis* by the differences in male and female frons as described below, by the more abundant, persistent setae on declivital interstriae 1 and 3, by the feeble granules on interstriae 2 near its apex, and by the larger average size. These populations are obviously closely allied and future collecting could discover intergradation between them.

Male.—Length 1.7 mm (paratypes 1.7–1.8 mm), 2.7 times as long as wide; color very dark brown.

Frons resembling *durangoensis* except much more broadly flattened, almost smooth, finely, rather closely punctured; setae on lateral margin much more abundant, longer, dorsal setae more broadly distributed.

Pronotum and elytral disc about as in *durangoensis*. Declivity with setae on interstriae 1 and 3 more regularly, closely placed, interstriae 3 with lower punctures feebly granulate; setae on striae 1 and 2 minute but present (obsolete in *durangoensis*).

FEMALE.—Similar to male except frons differing from female *durangoensis* by less strongly impressed, smoother dorsal area with a few rather coarse punctures, median carina stronger, separated from epistomal margin by half length of carina.

TYPE LOCALITY.—Xalapa, Veracruz, Mexico.

TYPE MATERIAL.—The male holotype, female allotype, and four paratypes were taken at the type locality on 10-VII-1983, No. 30, by Filipe A. Noguera.

The holotype, allotype, and paratypes are in my collection.

GENETIC VARIATION AND POPULATION STRUCTURE IN THE CLIFF CHIPMUNK, *EUTAMIAS DORSALIS*, IN THE GREAT BASIN OF WESTERN UTAH

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ABSTRACT.—Allelic variation at 21 of 39 electrophoretically resolved enzyme loci was used to examine patterns of geographic differentiation and population structure in six allopatric samples of *Eutamias dorsalis*. Coefficients of genetic similarity for paired combinations of *E. dorsalis* samples ranged from 0.955 to 0.975, except for one population that was 0.900. Conservative genic divergence among five populations is proposed to be the result of relatively recent isolation events. High positive F_{IS} values and chi-square analyses confirm a significant excess of homozygotes at several loci at the five localities for which sample sizes were statistically adequate. This may be partly attributable to inbreeding, a Wahlund effect, linkage disequilibrium, posttranslational modification, or some combination of these; but at present some of these alternatives cannot be excluded in favor of a single explanation. Some samples were collected across altitudinal gradients of over 800 m, suggesting that a Wahlund effect may be the most likely explanation for low levels of heterozygosity in these populations.

The distribution of montane mammals in the Great Basin of western Utah is disjunct, with populations isolated by low-elevation, cold desert valleys (Brown 1971a). The observed pattern has been explained by Pleistocene retreat (Late glacial to Late pleniglacial) of montane elements from pluvial valleys to higher elevation and more northern latitudes (Currey and James 1982, Wells 1983). At least four major glacial events occurred during the Pleistocene. The most recent, the Wisconsin, is suspected of having the greatest influence on existing boreal mammal faunas. Maximum glaciation occurred from the end of Early Pluvial (23,000 years B.P.) to Late Pluvial (12,500 years B.P.). During this time coniferous forests covered the foothills and piedmont, while low-elevation areas not covered by Lake Bonneville were dominated by sagebrush and juniper communities. Coniferous forests offered favorable dispersal habitat (Thompson and Mead 1982, Van Devender and King 1971, Wells and Berger 1967) in the intermountain valleys and low passes, which may have allowed exchange of montane faunal elements across the Great Basin.

The onset of xeric conditions during the Late Pluvial (12,500–7500 years B.P.) initiated major vegetation changes. Coniferous forests retreated upward in elevation and pinyon-juniper began to replace sagebrush communities from the south (Van Devender and Spaulding 1979). Continued warming during the Postpluvial (7,500–5,000 years B.P.) allowed range expansion of xeric mammal species in the low-elevation deserts, while ranges of small montane mammals followed vegetation shifts north and to montane uplands.

Recent biogeographic theory (Brown 1971a, 1978, Patterson 1980, 1982) suggests that distributions of small mammals can be explained as nonequilibrium extinctions without recolonization. Thus, the Great Basin environment and its insular montane mammal faunas offer interesting evolutionary "experiments" in which to assess the effects of isolation and possible recent population bottlenecking on levels of genetic divergence among conspecific montane mammal populations. The possibility of occasionally severe reductions in the sizes of insular mammal populations would be conducive to rapid fixation of alternate alleles and loss of overall genetic variability due to sampling error (Nei et al. 1975, Kilpatrick 1981), and this would facilitate divergence between populations despite their very recent isolation. This study reports on levels of genetic variability within and among samples of cliff chipmunks (*Eutamias dorsalis*) from six isolated mountain ranges in

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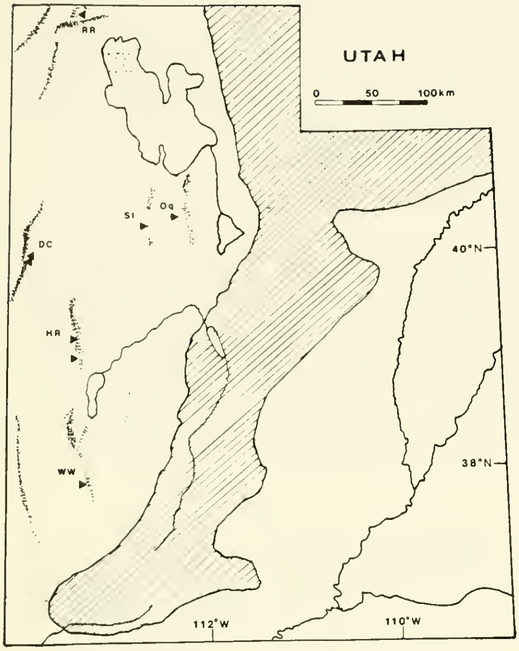

Fig. 1. Collection localities for *Eutamias dorsalis* from six mountain ranges in western Utah. Locality abbreviations are as in Table 1; stippled areas represent mountain ranges above 2,000 m; hatched region represents the Rocky Mountains.

western Utah, in an attempt to evaluate the effects of drift and recent insularization.

MATERIALS AND METHODS

A total of 90 specimens representing six allopatric populations of *Eutamias dorsalis* in the Great Basin of western Utah (Fig. 1) was collected from May through September 1983. All 90 voucher specimens were deposited in the Brigham Young University mammal collection as standard museum mounts. Collection location, population abbreviations and sample sizes, and voucher specimen numbers are presented in Table 1.

Preferred habitat of cliff chipmunks is open canopy pinyon-juniper complex on granite substrate (Brown 1971b). Chipmunk densities were low in all sites except two: Indian Farm Canyon of the Deep Creek Mountains and Painter Creek of the House Range. Low density in the Stansbury Range reflects the small area of suitable habitat. Two locations were sampled from both the House Range and the Deep Creek Mountains (Table 1, Fig. 1), but in each case specimens were assumed to be from one breeding population because of site proximity and habitat uniformity. Heart, liver, and blood tissues were immediately removed from live-trapped specimens (killed by cervical dislocation) and transported in liquid nitrogen to the laboratory. Tissues were then homogenized in an equal volume of buffer (0.01 M Tris, 0.001 M EDTA, 5×10^{-5} M NADP, pH adjusted to 7.0 with HCl), centrifuged for 20 min at 4 C, and stored at −80 C. Hemolysate was maintained at 0–5 C until assayed. Methods of horizontal starch gel electrophoresis and biochemical staining were similar to those described by Selander et al. (1971) and Harris and Hopkinson (1976), with minor modifications. Gels were prepared using a 14% concentration of hydrolysed starch, which consisted of a 1:1 mix of starch from Sigma Chemical Co. (lot 31F-0135) and Otto Hillers's Electrostarch (lot 307). A total of 39 presumptive gene loci was consistently resolved across all populations, and the buffer/stain combinations used are summarized in Table 2. Enzyme nomenclature follows recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984), with locus abbreviations following those suggested for lower vertebrates by Murphy and Crabtree (1985). We recognize that our nomenclature will depart from that used in most conventional mammal studies, but virtually all of these loci are either known (Fisher et al. 1980) or suspected of being homologous across all tetrapods (Harris and Hopkinson 1976).

Multilocus enzyme systems in which homologies are uncertain were simply designated numerically from most to least anodal (Est-"1", -"2", etc.). Alleles were designated numerically, with the most common allele assigned a value of 100 for anodal and −100 for cathodal migrants. Other allozymic bands and their corresponding alleles were designated as percentages of distances migrated relative to that of the 100 allele. Individual genotypes were inferred from enzyme phenotypes and statistically analyzed with the BIOSYS-1 program (Swofford and Selander 1981). Measures of genetic variability computed for each population include average locus heterozygosity (H, direct count), percent loci polymorphic (P), and mean number of alleles per locus (A).

TABLE 1. Summary of *Eutamias dorsalis* samples used in the study.

Locality	N	Elevation (m)	Museum deposition
DC = Deep Creek Mountains			
Indian Farm Canyon	22	1650–2400	BYU 7404–06,7409–28
Toms Creek	2	1800	BYU 7407–7408
HR = House Range			
Marjum Pass	18	1800–2100	BYU 7429–7446
Painter Creek	13	1800–2400	BYU 7447–7459
RR = Raft River Mountains			
Clear Creek	13	1800–2100	BYU 7471–7483
Oq = Oquirrh Mountains			
Ophir Canyon	11	1800–2250	BYU 7460–7470
WW = Wah Wah Mountains			
Pine Grove	9	1800–2250	BYU 7396–7403
St = Stansbury Mountains			
Johnson Pass	2	1800–1950	BYU 7484–7485

The genetic distance and similarity coefficients of Nei (1972, 1978) and Rogers (1972) were calculated for all pairwise comparisons of samples, and all such matrices were clustered by the UPGMA algorithm of Sneath and Sokal (1973). Wright's (1965, 1978) F-statistics were calculated for all variable loci, each population was tested for conformance to Hardy-Weinberg expectations using Levene's (1949) correction for small sample sizes, and intersample allele-frequency heterogeneity was evaluated by the contingency Chi-square method of Workman and Niswander (1970).

RESULTS

PATTERNS OF VARIABILITY.—Of the 39 loci scored in *E. dorsalis*, the following 18 loci were monomorphic for the same allele in all six populations: Adh-A, Ap-A, M-Aat-A, S-Aat-A, Pep-B, Pep-D, Esterases 1, 2, 4, and 5, Gpi-A, Gtdh-A, G3pdh-A, M-Icdh-A, Ldh-B, M-Mdh-A, Sod-"2", and P-alb. Allelic frequencies of the 21 polymorphic loci are given in Table 3. The Stansbury Mountain sample was fixed for S-Mdh-A, M-Me-A, and Xdh-A alleles that were rare or absent from the other samples. The Deep Creek sample varied at four loci, M-Acon-A, S-Icdh-A, Ldh-A, and Pgm-A, which were monomorphic for the common allele across all other samples. The remaining loci are characterized by differing degrees of polymorphism in different samples.

POLYMORPHISM AND HETEROZYGOSITY.—Table 3 summarizes estimates of the average proportion of polymorphic loci per sample (P), the average number of loci heterozygous per individual for each sample (H), and the mean number of alleles per locus (A). Estimates of P were calculated using both the .01 and .05 criteria in order to facilitate comparison with other investigators. The proportion of polymorphic loci per sample (P) averaged 0.15 (range: 0.05–0.25) and 0.20 (range: 0.05–0.33) for the .05 and .01 levels, respectively. Heterozygosity estimates averaged 0.010 and ranged from 0.005 in the Oquirrh sample to a high of 0.013 in the House Range sample. These estimates appear lower than other reports for this genus, H = 0.061 for *E. panamintus* (Kaufman et al. 1973). Estimates of A ranged from 1.143 for the Stansbury sample, which may be an artifact of small sample size, to a high of 1.857 for the Deep Creek sample. The average across all samples was 1.524.

GENETIC SIMILARITY AND DISTANCE.—Coefficients of genetic similarity, S (Rogers 1972), and genetic distance, D (Nei 1978), based on the 39 loci assayed were calculated for all pairwise sample comparisons (Table 4). Values of S ranged from 0.891 to 0.976 and for D from 0.001 to 0.086. The Stansbury sample consistently had the lowest S and highest D values. Values from the matrices of intersample genetic similarities and distances were clustered by the UPGMA option of BIOSYS-1, and dendrograms are presented in Figure 2 (dendrograms of Nei's [1978] I matrix and Nei's [1972] earlier I and D coefficients are available from the senior author upon

TABLE 2. Enzymes and electrophoretic conditions used in the analysis of *Eutamias dorsalis* populations. Locus prefixes M and S refer to mitochondrial and supernatant (= cytosolic) loci, respectively; and tissue abbreviations H, He, L, and P refer to heart, hemolysate, liver, and plasma, respectively. Abbreviations of enzymes in parentheses are older names found in most mammal literature.

Enzyme	Enzyme commission number[1]	Locus	Buffer conditions[2]	Tissue
Aconitate hydratase	4.2.1.3	M-Acon-A	B	L
Alcohol dehydrogenase	1.1.1.1	Adh-A	B	L
Aminopeptidase ("Lap")	3.4.11.1	Ap-A	A	P
Aspartate aminotransferase ("Got-2")	2.6.1.1	M-Aat-A	B	L
Aspartate aminotransferase ("Got-1")	2.6.1.1	S-Aat-A	B	L
Dipeptidase[3]	3.4.12.9	Pep-A	B	L
Dipeptidase	3.4.13.9	Pep-B	B	L
Dipeptidase	3.4.13.9	Pep-D	B	L
Esterases (non-specific)	—	Est. "1"-"6"	D	L,P
Fumarate hydratase	4.2.1.2	Fum-A	B	L
Glucose dehydrogenase	1.1.1.47	Gcdh-A	B,C	L
Glucose-6-phosphate isomerase ("Pgi")	5.3.1.9	Gpi-A	B	L
Glucose-6-phosphate dehydrogenase	1.1.1.49	G6pdh-A	B	L
Glutamate dehydrogenase	1.4.1.2	Gtdh-A	B	L
Glycerol-3-phosphate dehydrogenase ("-Gpd")	1.1.1.8	G3pdh-A	B	L
L-Iditol dehydrogenase ("Sdh")	1.1.1.14	Iddh-A	B	L
Isocitrate dehydrogenase ("Idh-2")	1.1.1.42	M-Icdh-A	B	L
Isocitrate dehydrogenase ("Idh-1")	1.1.1.42	S-Icdh-A	B	L
Lactate dehydrogenase ("Ldh-2")	1.1.1.27	Ldh-A	C	L
Lactate dehydrogenase ("Ldh-1")	1.1.1.27	Ldh-B	C	L
Malate dehydrogenase ("Mdh-2")	1.1.1.37	M-Mdh-A	B	L
Malate dehydrogenase ("Mdh-1")	1.1.1.37	S-Mdh-A	B	L
"Malic enzyme"[4] ("Me-2")	1.1.1.40	M-Me-A	B	L
"Malic enzyme" ("Me-1")	1.1.1.40	S-Me-A	B	L
Mannose-6-phosphate isomerase	5.3.1.8	Mpi-A	B	L
Phosphoglucomutase	5.4.2.2	Pgm-A	B	L
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh-A	B	L
Superoxide dismutase ("Ipo")	1.15.1.1	Sod-"1"[5]	B	L
Superoxide dismutase ("Ipo")	1.15.1.1	Sod-"2"	D	L
Xanthine dehydrogenase	1.2.1.37	Xdh-A	B	L
General proteins:				
Albumin	—	Alb	A	L,H
Hemoglobin[6]	—	Hb-"1"	A	He
Post-albumin	—	P-alb	A	L,H
Transferin	—	Trf	A	L,H

[1] Nomenclature and E.C. numbers follow recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984).

[2] Buffers used: A—Tris-hydrochloric acid pH 8.5, 50 ma for 5 hr; B—Tris-citrate pH 8.0, 75 ma for 6 hr; C—Tris-citrate pH 6.7, 50 ma for 6 hr; D—Poulik pH 8.7, 50 ma for 10 hr.

[3] Substrates for dipeptidases A, B, and D were glycyl-L-leucine, DL-leucylglycylglycine, and L-phenylalynyl-L-proline, respectively.

[4] NADP-dependent malate dehydrogenase

[5] Locus homologies with lower vertebrates uncertain

[6] *Eutamias* hemoglobin is encoded by two loci (Jensen et al. 1975), but the single locus resolved in this study is arbitrarily designated Hb-"1".

request). In all dendrograms generated, five samples are very similar (S values 0.94–0.98) and consistently cluster in one branch, whereas the Stansbury Mountain sample is comparatively very divergent (average S = 0.90).

POPULATION STRUCTURE.—A summary of F statistics for all variable loci is presented in Table 5, excluding those for the small Stansbury sample. The inbreeding coefficients (F_{IS}) ranged from −0.016 to 1.000 with a mean of 0.320. The standardized gene frequency variance (F_{ST}) values ranged from 0.013 to 0.196 with a mean of 0.094.

Chi-square tests were performed to test for deviation of genotypes from Hardy-Weinberg expectations for all variable loci in all but the Stansbury sample, and surprisingly, all samples showed significant deviation at some loci, due to the presence of rare homozygotes. The House Range sample, for example, had no heterozygotes at G-6–pdh (30 100/100 and 1

TABLE 3. Allele frequencies and estimates of genic variability in six samples of *Eutamias dorsalis*. Locality abbreviations are from Table 1 and Figure 1.

		Sample sizes and localities					
Locus	Allele	(N=9) WW	(N=24) DC	(N=11) Oq	(N=13) RR	(N=31) HR	(N=2) St
M-Acon-A	88	0.0	0.042	0.0	0.0	0.0	0.0
	100	1.000	0.958	1.000	1.000	1.000	1.000
Est-"3"	86	0.167	0.125	0.0	0.0	0.0	0.0
	100	0.556	0.875	0.545	1.000	0.871	0.500
	107	0.222	0.0	0.455	0.0	0.129	0.250
	105	0.056	0.0	0.0	0.0	0.0	0.000
	110	0.0	0.0	0.0	0.0	0.0	0.250
Est-"6"	90	0.278	0.083	0.091	0.154	0.194	0.0
	100	0.556	0.792	0.545	0.692	0.710	0.500
	105	0.167	0.083	0.364	0.077	0.097	0.500
	110	0.0	0.042	0.0	0.077	0.0	0.0
Fum-A	100	1.000	0.875	1.000	0.962	0.887	1.000
	188	0.0	0.125	0.0	0.038	0.113	0.0
Gcdh-A	100	1.000	1.000	1.000	1.000	0.968	1.000
	110	0.0	0.0	0.0	0.0	0.032	0.0
G6pdh-A	100	1.000	1.000	1.000	1.000	0.968	1.000
	108	0.0	0.0	0.0	0.0	0.032	0.0
S-Icdh-A	100	1.000	0.979	1.000	1.000	1.000	1.000
	112	0.0	0.021	0.0	0.0	0.0	0.0
Iddh-A	100	1.000	0.938	1.000	0.962	1.000	1.000
	387	0.0	0.062	0.0	0.038	0.0	0.0
Ldh-A	100	1.000	0.958	1.000	1.000	1.000	1.000
	125	0.0	0.042	0.0	0.0	0.0	0.0
S-Mdh-A	84	0.0	0.0	0.0	0.038	0.0	1.000
	100	1.000	1.000	1.000	0.924	1.000	0.0
	105	0.0	0.0	0.0	0.038	0.0	0.0
M-Me-A	75	0.0	0.167	0.091	0.077	0.0	1.000
	100	1.000	0.813	0.909	0.923	1.000	0.0
	110	0.0	0.020	0.0	0.0	0.0	0.0
S-Me-A	50	0.0	0.208	0.0	0.0	0.065	0.0
	100	1.000	0.792	1.000	1.000	0.935	1.000
Mpi-A	100	1.000	1.000	0.955	1.000	0.935	1.000
	115	0.0	0.0	0.045	0.0	0.065	0.0
Pep-A	100	1.000	1.000	1.000	1.000	0.984	1.000
	120	0.0	0.0	0.0	0.0	0.016	0.0
Pgm-A	35	0.0	0.083	0.0	0.0	0.0	0.0
	100	1.000	0.917	1.000	1.000	1.000	1.000
Pgdh-A	118	0.333	0.0	0.0	0.0	0.0	0.0
	100	0.667	1.000	1.000	1.000	1.000	1.000
Sod-"1"	60	0.111	0.0	0.143	0.0	0.0	0.0
	100	0.889	0.771	0.714	0.846	0.968	1.000
	130	0.0	0.229	0.143	0.154	0.032	0.0
Xdh-A	40	0.0	0.166	0.182	0.077	0.0	1.000
	100	1.000	0.792	0.818	0.923	1.000	0.0
	110	0.0	0.042	0.0	0.0	0.0	0.0
Alb	100	0.889	1.000	1.000	1.000	1.000	1.000
	110	0.111	0.0	0.0	0.0	0.0	0.0
Hb-"1"	80	0.056	0.020	0.0	0.0	0.065	0.0
	100	0.944	0.917	0.955	0.923	0.903	1.000
	120	0.0	0.063	0.045	0.077	0.032	0.0

Table 3 continued.

		Sample sizes and localities					
Locus	Allele	(N=9) WW	(N=24) DC	(N=11) Oq	(N=13) RR	(N=31) HR	(N=2) St
Trf	100	0.889	1.000	1.000	1.000	0.968	1.000
	120	0.111	0.0	0.0	0.0	0.032	0.0
Polymorphic per sample (P)*	(.05)	0.179	0.256	0.128	0.154	0.154	0.051
	(.01)	0.179	0.325	0.175	0.200	0.275	0.051
Average heterozygosity per individual (H)**		0.048	0.024	0.042	0.028	0.036	0.050
Mean number of alleles per locus (A)		1.476	1.857	1.478	1.571	1.619	1.143

*A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95 (.05 criterion) or 0.99 (.01 criterion).
**Estimate of H determined by direct count.

TABLE 4. Matrix of genetic similarity S (Rogers 1972) above the diagonal and genetic distance D (Nei 1978) below the diagonal for six samples of *E. dorsalis*. Abbreviations of populations follow Table 1.

Population	WW	DC	Oq	RR	HR	St
Wah Wah Mtns.	—	0.941	0.962	0.963	0.965	0.891
Deep Creek Mtns.	0.010	—	0.959	0.969	0.964	0.891
Oquirrh Mtns.	0.004	0.007	—	0.969	0.964	0.912
Raft River Mtns.	0.006	0.002	0.006	—	0.976	0.901
House Range	0.005	0.003	0.005	0.001	—	0.894
Stansbury Mtns.	0.086	0.071	0.066	0.075	0.085	—

108/108 genotypes) and Sod-"1" (30 100/100 and 1 130/130), $X^2 = 61.02$ (1 df), $P < .001$. Samples from the Oquirrh, Raft River, and Wah-Wah Mountains had no heterozygotes at three loci each, as follows: (1) Oq—M-Me-A (10 100/100 and 1 75/75, $X^2 = 21.05$ with 1 df), Sod-"1" (5 100/100, 1 60/60, and 1 130/130; 4 individuals unscorable; $X^2 = 26.22$ with 1 df), Xdh-A (9 100/100 and 2 40/40, $X^2 = 14.12$ with 1 df), $P < .001$; (2) RR—M-Me-A (12 100/100 and 1 75/75, $X^2 = 25.04$ with 1 df), Sod-"1" (11 100/100 and 2 130/130, $X^2 = 16.76$ with 1 df), Xdh-A (12 100/100 and 1 40/40, $X^2 = 14.12$ with 1 df), $P < .001$; (3) WW—Pgdh-A (6 100/100 and 3 118/118, $X^2 = 10.47$ with 1 df), Sod-"1" (8 100/100 and 1 60/60, $X^2 = 17.01$ with 1 df), Trf (8 100/100 and 1 120/120, $X^2 = 17.01$ with 1 df), $P < .001$. The same trend was evident in 8 of 13 polymorphic loci in the Deep Creek sample: M-Acon-A (23 100/100 and 1 88/88, $X^2 = 47.02$ with 1 df), Ldh-A (23 100/100 and 1 125/125, $X^2 = 47.02$ with 1 df), Pgm-A (22 100/100 and 2 35/35, $X^2 = 31.38$ with 1 df), Fum-A (21 100/100 and 3 188/188, $X^2 = 28.27$ with 1 df), S-Me-A (19 100/100 and 5 50/50, $X^2 = 26.25$ with 1 df), Sod-"1" (19 100/100 and 5 130/130, $X^2 = 26.25$ with 1 df); M-Me-A (19 100/100, 4 75/75, and 1 100/110, $X^2 = 26.96$ with 3 df); Xdh-A (19 100/100, 4 40/40, and 1 110/110, $X^2 = 73.99$ with 3 df); $P < .001$ in all cases.

DISCUSSION

Allopatric populations of cliff chipmunks sampled had weak interpopulational divergence (average $D = 0.028$), with the Stansbury sample strongly divergent from others (average $D = 0.74$) while the remaining samples are only slightly divergent from each other (average $D = 0.005$, Fig. 2). The small D values are consistent with those calculated for other mountain-top species of small rodents (Mewaldt and Jenkins 1986, Sullivan 1985). The divergence of the Stansbury Mountain sample is primarily due to the fixation of three alleles, S-Mdh-A (84), M-Me-A (75), and Xdh-A (40) (Table 3) that were rare or absent in the rest of the samples. This sample also had a unique Est-3 (110) allele at 0.25 frequency, but because of its small size (2 individuals), some of this difference may simply be a function of a large sampling error. However, the Stansbury population is likely

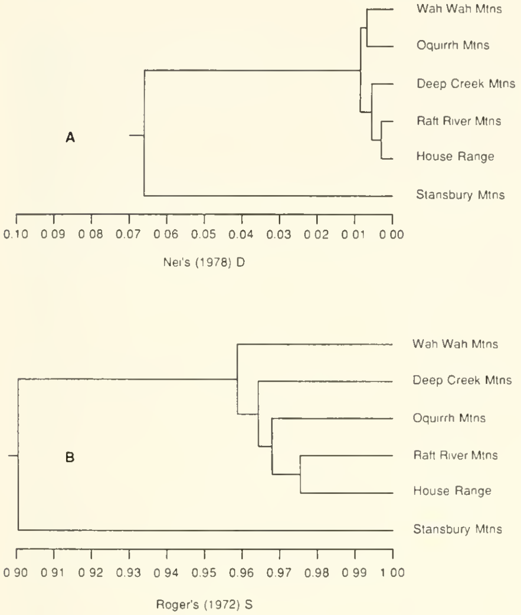

Fig. 2. UPGMA dendrograms of genetic distance values (Nei 1978), A, and similarity values (Rogers 1972), B, for six samples of *Eutamias dorsalis*. Sample localities are those shown in Figure 1; cophenetic correlation values are 0.991 and 0.975, respectively.

Table 5. Summary of F-statistics for all variable loci across all examined samples of *Eutamias dorsalis* except Stansbury Mountains.

Locus	F_{IS}	F_{IT}	F_{ST}
M-Acon-A	1.000	1.000	0.034
Est-"3"	−0.259	−0.002	0.196
Est-"6"	−0.211	−0.148	0.052
Fum-A	0.517	0.544	0.056
Gcdh-A	−0.033	−0.006	0.026
G-6-pdh-A	1.000	1.000	0.027
S-Icdh-A	−0.021	−0.004	0.017
Iddh-A	−0.056	−0.021	0.034
Ldh-A	1.000	1.000	0.034
S-Mdh-A	−0.061	0.012	0.047
M-Me-A	0.933	0.937	0.066
S-Me-A	0.714	0.750	0.127
Mpi-A	−0.060	−0.022	0.035
Pep-A	−0.016	−0.003	0.013
Pgm-A	1.000	1.000	0.068
Pgdh-A	1.000	1.000	0.286
Sod-"1"	1.000	1.000	0.068
Xdh-A	1.000	1.000	0.083
Alb	−0.125	−0.023	0.091
Hb-"1"	−0.072	−0.058	0.013
Trf	0.752	0.770	0.071
Mean	0.320	0.384	0.094

very small, as evidenced by very low capture success per unit effort compared to other samples, and it appears to be restricted to one canyon. Thus, the relatively large level of genetic divergence may also reflect the influence of a recent population bottleneck and/or pronounced genetic drift.

The overall mean F_{ST} value of 0.094 (Table 5) suggests an appreciable level of subdivision between the montane populations, although much higher levels are known in other small mammals ($F_{ST} = 0.412$ for *Thomomys bottae*, for example; see Patton and Yang 1977). Appreciable substructuring in populations may result from population bottlenecks and the ensuing influence of drift (Schwartz and Armitage 1980), and the winter of 1982–83 was one of the most severe on record in Utah (NOAA 1983). This may have reduced population sizes, forcing inbreeding and fostering a breeding structure in which drift could have a pronounced influence. However, if we invoke an explanation of differentiation by climatically caused population bottlenecking and subsequent drift for the Stansbury sample, we must also account for the extensive polymorphism observed in the other samples (e.g., DC and HR), which presumably were also subject to the same severe conditions. It is unlikely that the observed polymorphism of alternate alleles could have been accumulated in each population in the short time since the Postpluvial, 7500 years B.P., when desert advancement last isolated mountain ranges. Two alternate explanations are proposed. First, one large, genetically variable population may have been widely distributed across the Great Basin and subsequently became fragmented and restricted to mountain ranges by the Pleistocene climatic shifts. This is the vicariance explanation proposed by Patterson (1980, 1982) for montane mammal populations in New Mexico. This hypothesis would predict near genetic uniformity and very low between-population divergence in the absence of drift, isolation by distance (Wright 1965), or some behavioral mechanism contributing to small, effective breeding sizes and nonrandom mating. Alternately, since chipmunks are reported from the Pliocene of North America (Black 1972), *E. dorsalis* as a species may predate the Pleistocene and may have entered the Great Basin from the Rocky Mountains or some other center of origin. Pleistocene ice ages repeatedly forced floral and faunal elements to lower elevations and may have facilitated intermittent gene flow among chipmunk populations. This may have been sufficient to maintain allelic variants in most populations. Without additional genetic information from hypothesized source populations (i.e., Wasatch Range) and others more distantly isolated in Great Basin mountain ranges, we cannot choose among these alternatives.

Ecological and behavioral factors may be as important as historical events in determining the genetic structure of chipmunk populations. For example, in addition to the dispersal barriers between populations (i.e., desert valleys, lakes, rivers, and distance), chipmunks also face problems of short-distance dispersal imposed by complex, interspecific competition, interspecific territoriality (Broadbooks 1970, Brown 1971b, Heller 1971), habitat requirements (Sharples 1983), predation, altitudinal zonation (Chappell 1978, Heller 1971), and philopatry to home range (Broadbooks 1970, Martinsen 1968, Sheppard 1972). Broadbooks (1970), Martinsen (1968), and Sheppard (1971) found three significant behavioral characteristics of yellow-pine chipmunks (*E. amoenus*) and least (*E. minimus*) chipmunks that would influence the geographic distribution of allele frequencies: (1) chipmunks have a well-defined home range in which they remain from year to year, (2) a high percentage (8 of 11) of the offspring remain in the area of the parent, and (3) 67.4% of chipmunks released .4 km from their home range returned within 1–3 days after release.

If similar behavior is typical of *E. dorsalis* populations, then breeding units may be characterized by high incidences of parent-offspring or sib matings. Some evidence of inbreeding is given by the F-statistics. For example, when averaged across all samples, F_{IS} values were mostly high and positive, an indication of heterozygote deficiency for many loci (Table 5). This is due to the complete absence of heterozygotes at some loci in the five localities for which sample sizes were statistically "adequate" (all but Stansbury). The F_{IS} values may reflect either high levels of inbreeding or further levels of subdivision within our "samples" of *E. dorsalis*, but other explanations are possible. For example, the frequent occurrence of double homozygotes in some loci segregating three alleles (Xdh-A and S-Me-A in the Deep Creek sample, and Sod-"1" in the Oquirrh Mountain sample) also suggests the possibility of linkage disequilibrium in small, nonrandom mating populations. Several other studies have shown that small population size per se is not always accompanied by strong inbreeding, as various species of mammals avoid consanguinous matings by a number of behavioral mechanisms (Foltz and Hoogland 1983, Hoogland 1982, Patton and Feder 1981, Schwartz and Armitage 1980). Patton and Feder (1981), for example, found a paradoxical situation in which high heterozygosity was maintained in apparently very small breeding units of the gopher *Thomomys bottae*, and this was explained as an equilibrium achieved between the rate of migration (either recolonization following extinction or individual recruitment into groups) and the effective number of individuals that are contributing to the breeding effort each year. We do not have the ecological or pedigree information necessary to evaluate the importance of these factors in *E. dorsalis*, but their prevalence in other rodents, and the previously mentioned behavioral traits of other *Eutamias*, collectively suggest that inbreeding alone cannot explain all of the observed heterozygote absences in these populations. If it did, it should have a more or less equal influence across all variable loci, and this is not the case (Table 3).

Alternatively, the high frequency of fixed allelic differences among different individuals within the same sample suggests that we may well have pooled breeding units that differed drastically in their allelic composition (Wahlund effect). The Deep Creek sample displayed heterozygote deficiencies at eight loci and was comprised of collections from two different localities (Table 1, Fig. 1), but the excess number of homozygotes in the total sample did not correlate with the numbers of individuals from either of these two sites. In other words, this effect did not disappear when these samples were analyzed separately. Similarly, the House Range sample was collected from two localities and showed heterozygote deficiencies at five loci; again the phenomenon was independent of sample localities. The Oquirrh and Raft River samples were collected from one canyon each, and both samples showed heterozygote deficiencies at the same three loci (S-Me-A, Sod-"1", and Xdh-A). Chesser (1983) has shown that important patterns of genetic variability may be obscured when breeding units are pooled together, and we suspect that our "samples" of *E. dorsalis* may include separate Mendelian units that may differ drastically in allelic composition at some loci.

We recognize the risk of over-analyzing these data in light of the small sample sizes but feel that at least some other possible explanations for the complete absence of heterozygotes at many loci can be ruled out. The possibilities include: (1) inadvertant inclusion of a second species of *Eutamias* in the samples, (2) scoring of multiple loci for some enzyme systems in only select individuals from each sample, and (3) enzyme denaturation and/or posttranslational modification of gene products in select individuals.

Eutamias minimus is sympatric with *E. dorsalis* at all localities sampled, but the latter is very distinct, and CLP and MLD have had considerable experience with both species. Museum voucher specimens were prepared for all individuals used in this study, and a recheck confirmed their identification as *E. dorsalis*. We conclude that there is almost no chance of "mistaken identity" and that this explanation would not, by itself, account for the different locus *combinations* displaying heterozygote absence at the five localities tested.

Second, we can rule out the likelihood of scoring different loci from a multilocus enzyme in different individuals from the same populations, because the number of loci encoding the enzymes used in this study is well known in mammalian systems (Harris and Hopkinson 1976). A single tissue type was used in most electrophoretic runs (liver, see Table 2), but even when others were used, multilocus systems were evident either as two zones of activity on the same gel, or as different patterns of variability evident in different tissues of the same individual. The rare homozygotes we resolved were scored as such from zones of different mobility in one or a few individuals on gels that otherwise contained a single electromorph common to all other specimens, with the *same* tissue type being used throughout.

The problem of enzyme denaturation and/or posttranslational modification is more difficult to assess. Moore and Yates (1983) evaluated rates of protein inactivation (for 27 enzymes) under controlled conditions in four species of mammals of varying body size (*Antilocapra americana*, *Plecotus townsendii*, *Dipodomys ordii*, and *Peromyscus boylii*) and found that 95% of the proteins routinely examined electrophoretically are still stable (i.e., not denatured and showing mobilities identical to controls) in unfrozen tissues for a minimum of 12 hrs after death. The locus Sod-"1" had no heterozygotes in all five of the *E. dorsalis* samples but was one of the most stable systems studied by Moore and Yates (1983); the least stable system examined by them, ADH, was not included in our protocol (Table 2). Further, our method of obtaining animals from the field insured that tissues were taken from specimens and frozen in liquid nitrogen within 30 min of capture. Laboratory protocol for homogenizing and storing tissue samples was consistent throughout the study, so there seems to have been little opportunity for extensive contamination or denaturation of the samples.

The possibility of epigenetically or posttranslationally modified electromorph mobilities (see Lebherz 1983) in some *E. dorsalis* specimens is one that we cannot evaluate with the information we have. Some classes of these alterations are known to have a genetic basis in some organisms (Womack 1983, Dykhuizen et al. 1985), and in at least one rodent species, mobility differences in two different loci (Trf and Ap-A) seem to vary with the physiological state of the animal (McGovern and Tracy 1981). If this is the explanation for most or all of the rare homozygotes we encountered, then the physiologically or genetically based phenomenon for such electromorph mobility alterations must be widespread in *E. dorsalis* populations. Elimination of these individuals from our analyses would lower the mean inbreeding coefficient (F_{IS}) and perhaps slightly decrease mean D and F_{ST} values, although our conclusions about a moderate level of population subdivision and minimum genetic divergence would be virtually unaltered.

We suggest that the montane mammal populations of the Great Basin offer excellent model systems for addressing issues in island biogeography and population biology, but that future sampling strategies be designed to collect an adequate number of individuals (n = 25, if possible) from a single ecologically homogenous site, and that, for larger mountain ranges at least, two or more localities be collected and analyzed as separate population samples in order to assess within, as well as between, mountain range divergence. Such control in sampling will allow for a more rigorous assessment of macrogeographic patterns of gene flow and population structure.

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OBSERVATIONS ON THE ECOLOGY AND TROPHIC STATUS OF LAKE TAHOE (NEVADA AND CALIFORNIA, USA) BASED ON THE ALGAE FROM THREE INDEPENDENT SURVEYS (1965–1985)

Sam L. VanLandingham[1]

ABSTRACT.—Numerous physical, chemical, and biological criteria evidently confirm that Lake Tahoe is oligotrophic. However, detailed examination of the ecology and trophic status of algae (mostly diatoms) from Lake Tahoe taken from three independent, long-term sampling programs aided in interpretation of plankton and periphyton algal communities by spectral analysis (supported by computerized data synthesis) and suggested that the prevailing trophic disposition of this deep, subalpine lake no longer can be described as "ultra-oligotrophic" or typically oligotrophic. Although at various places in recent years there has been some increase in oligotrophic species that seems to correspond with recent sewage export from the Tahoe basin, there was a marked tendency toward mesotrophy and/or eutrophy over most of the lake from April 1965 through October 1985. This study posits the speculation that there may be other "ultra-oligotrophic" lakes over the world from which future studies may reveal algal communities that may be described as more mesotrophic and/or eutrophic than oligotrophic. Lake Tahoe probably is not as oligotrophic as is generally believed, and the indicator algae in it are not as accurate as is generally believed.

There have been few American lakes that have inspired such curiosity, commentary, lore, and interest among scientists as Lake Tahoe. From the time of Ehrenberg (1871), there has been considerable controversy and speculation in connection with the limnology of Lake Tahoe. Statements describing Lake Tahoe as "a remarkably unproductive subalpine environment" (Mahood et al. 1984) and as "still one of the most oligotrophic lakes in the world" (Goldman 1974) seem misleading; on the other hand, such comments as "heavy periphyton growth" and "alarming increase in primary productivity" (Goldman and De Amezaga 1975) and "it is beginning to show signs of the earliest stages of eutrophication" (Mahood et al. 1984) are equally perplexing. In addition, Goldman (1981) reported that the annual productivity of the pelagial water of Lake Tahoe has more than doubled in the past two decades. Moreover, I find the terming of Lake Tahoe as "extremely oligotrophic" (Goldman and Armstrong 1969) and "ultra-oligotrophic" (Tilzer and Horne 1979) enigmatic in view of the obvious enrichment of the littoral areas. Indications of mesotrophy and eutrophy demonstrated by the algae in the lake are conspicuous, and Tahoe no longer can be considered "one of the most oligotrophic lakes in the world."

The California-Nevada–Federal Water Pollution Control Administration (FWPCA) survey confirmed that Lake Tahoe was oligotrophic mainly on the basis of low zooplankton and phytoplankton counts, low periphyton densities, and low P (5 $\mu g\ l^{-1}$) and N (100 $\mu g\ l^{-1}$) concentrations. A large number of species in Lake Tahoe was described as eutrophic, although their presence was not considered to be indicative of eutrophic conditions (California Department of Water Resources 1966). Total P at many stations in the last 10–15 years seems excessive for an oligotrophic lake and probably has enhanced the growth of many eutrophic diatoms and other algae. Why are so many of the typical or cosmopolitan oligotrophic diatoms, such as *Melosira distans* (Ehr.) Kütz., *Cyclotella ocellata* Pant., *Frustulia rhomboides* (Ehr.) De Toni, *Navicula radiosa* Leud.-Fort., *Pinnularia biceps* Greg., *Tabellaria flocculosa* (Roth) Kütz., and *Tetracyclus lacustris* Ralfs, infrequent or rare in Lake Tahoe? All of these taxa are common in both ancient and modern lakes in this region. *Melosira distans*, for example, is a dominant or subdominant species in oligotrophic Suttle and Woahink lakes, Oregon, in a Pleistocene oligotrophic diatomite deposit about 500 m from the shore of Lake Tahoe at Tahoe City, and in several oligotrophic dry lakes nearby in Nevada. The rarity of the above-mentioned diatoms can be explained partially by the observation that most of these taxa prefer acidic waters and that Lake Tahoe nearly always has a pH above 7. Only a very few oligotrophic diatoms, such as *Cyclotella stelligera* (Cl.) V.H., *Achnanthes minutissima* Kütz., and *Anomoeoneis exilis* (Kütz.) Cl., ever attain noteworthy prominence in Lake Tahoe. Weber (1970) used plankton counts of less than 500 cells/ml as one of many criteria for determining oligotrophic lakes. In recent years cell counts for the planktonic algae occasionally have exceeded 500 cells/ml in littoral areas.

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Problems associated with interpreting trophic or inorganic nutrient categories in lakes are numerous. Whiteside (1983) contends that the oligotrophy-eutrophy concept is best interpreted in its original sense, namely, referring to nutrient levels (or community structure) in lakes, and is inappropriately used when referring to the aging process, morphometry, etc. It follows that it may be possible for a lake to be deep or in the youthful stages of ontogeny but have relatively high nutrient levels. Or, a lake may be shallow or in the oldest stages of ontogeny but have lower nutrient levels. Sometimes lakes defy assignment to a definite trophic status as La Perriere et al. (1975) demonstrated in respect to a deep, subarctic lake. The occurrence of certain diatoms, which generally are considered eutrophic, seems to be influenced more by such factors as temperature than by trophic levels. For instance, Weber (1973) pointed out that *Melosira islandica* O. Müll. is considered eutrophic in northern Europe, but in North America it is found only in cold, oligotrophic water both in higher latitudes and higher altitudes at lower latitudes. *Fragilaria pinnata* Ehr. and *F. crotonensis* Kitt. are examples of diatoms that generally are considered eutrophic but that occur commonly in oligotrophic lakes (California Department of Water Resources 1966). No matter what the descriptive or semantic status of Lake Tahoe may be, there is good evidence that its algae frequently indicate relatively moderate to high nutrient levels, and they apparently have done so for many years.

COMPUTER DATA SYNTHESIS

Continuous algal ecological spectral analysis reference system (CAESARS) is a comprehensive, computerized retrieval plan based on approximately 3,000 publications from which about 500,000 bits of information concerning over 4,000 common and widely occurring algae taxa are categorized into nine physical, chemical, and occurrence spectra, each of which is subdivided into four or more categories (Figs. 1–4). Categories of each spectrum are based on theoretical and natural observations found in Kisseleva (1939), Foged (1963), Reimer (1965), Round (1965), De Smet and Evens (1972), Schoeman (1973), Friedrich (1973), Lowe (1974), and Temniskova-Topalova and Misaleva (1982). Important expoundings on each of the nine spectra are: pH (Hustedt 1937, Meriläinen 1967, Cholnoky 1968), saprobian (Kolkwitz and Marsson 1908, Caspers and Schulz 1960, Fjerdingstad 1964, 1965a, 1965b, Caspers and Karbe 1967, Sládeček 1967, 1969, 1973, Schoeman 1979, Lange-Bertalot 1979a, 1979b), nutrient (Rawson 1956, Sparling and Nalewajko 1970), halobion (Kolbe 1927, Legler and Krasske 1940), current (Shirshov 1933, Zelinka and Marvan 1961, Blum 1963), general habitat, specific habitat, and seasons (Schröder 1939, Whitford and Schumacher 1963, Hutchinson 1967, Symons 1970, Staker 1976, Pudo 1979, Moore 1981), and temperature (Louis and Aelvoet 1969, Friedrich 1973). Information from new references is used continuously to update CAESARS. Most terminology used in the categories of the spectra is self-explanatory or in common use, but Lowe (1974) and VanLandingham (1982) give detailed descriptions of each category and spectrum. A series of histograms can be made (Figs. 1–4) by calculating the percentage of each taxon in each sample and totaling the percentages of all taxa in each category. These spectral categories and/or histograms have proven to be ideal as a standard of ecological comparison for various algal samples from all over the world (Collingsworth et al. 1967, Duthie and Rani 1967, VanLandingham 1968, 1970, 1972, 1976, 1982, Messina-Allen and VanLandingham 1970, Robbins and Hohn 1972, VanLandingham and Jossi 1972, Abbott and VanLandingham 1972, Lowe

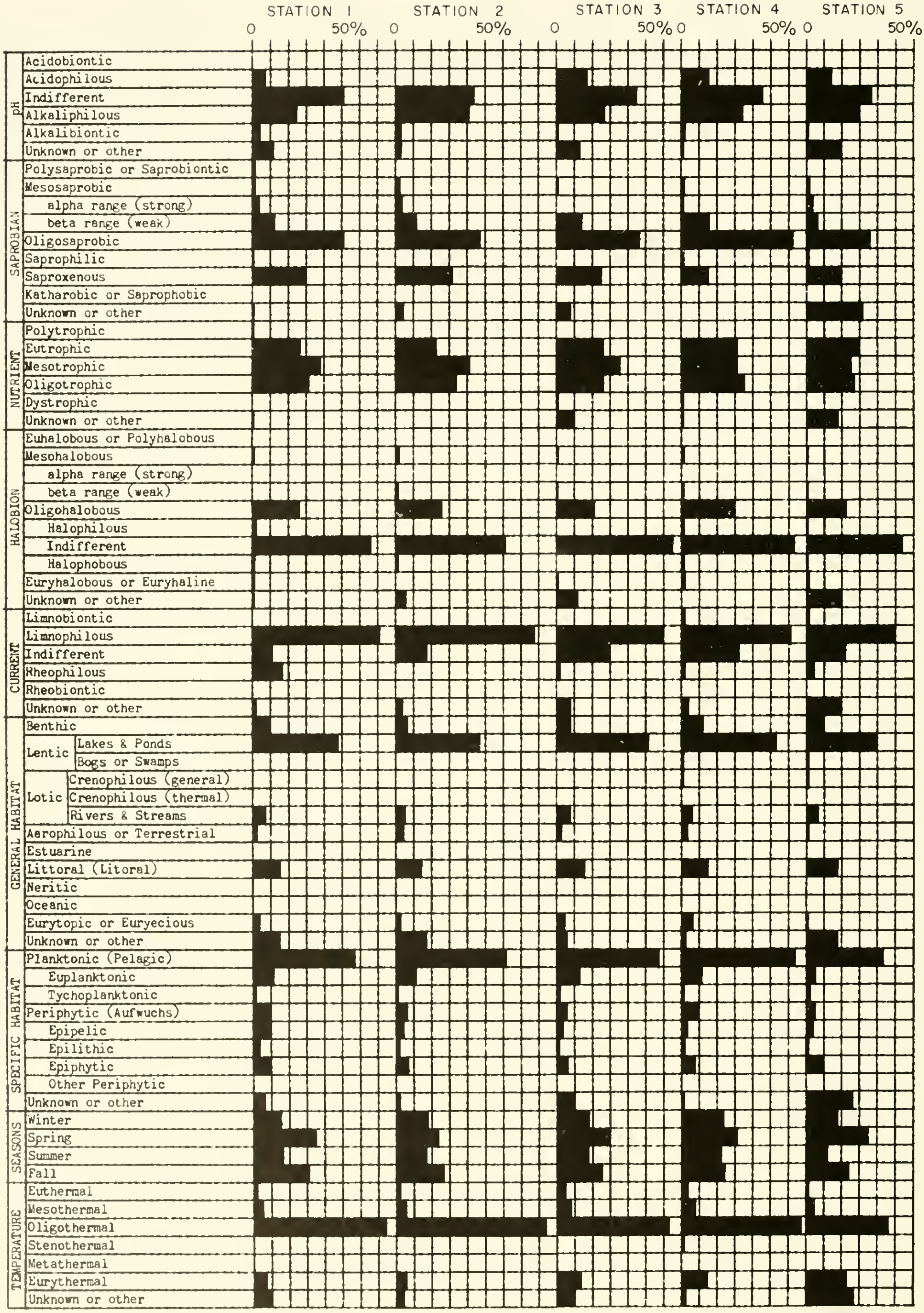

Fig. 1. Spectral histograms based on diatom species percentages from plankton grab samples on 6–8 February 1967 by the California-Nevada–FWPCA survey.

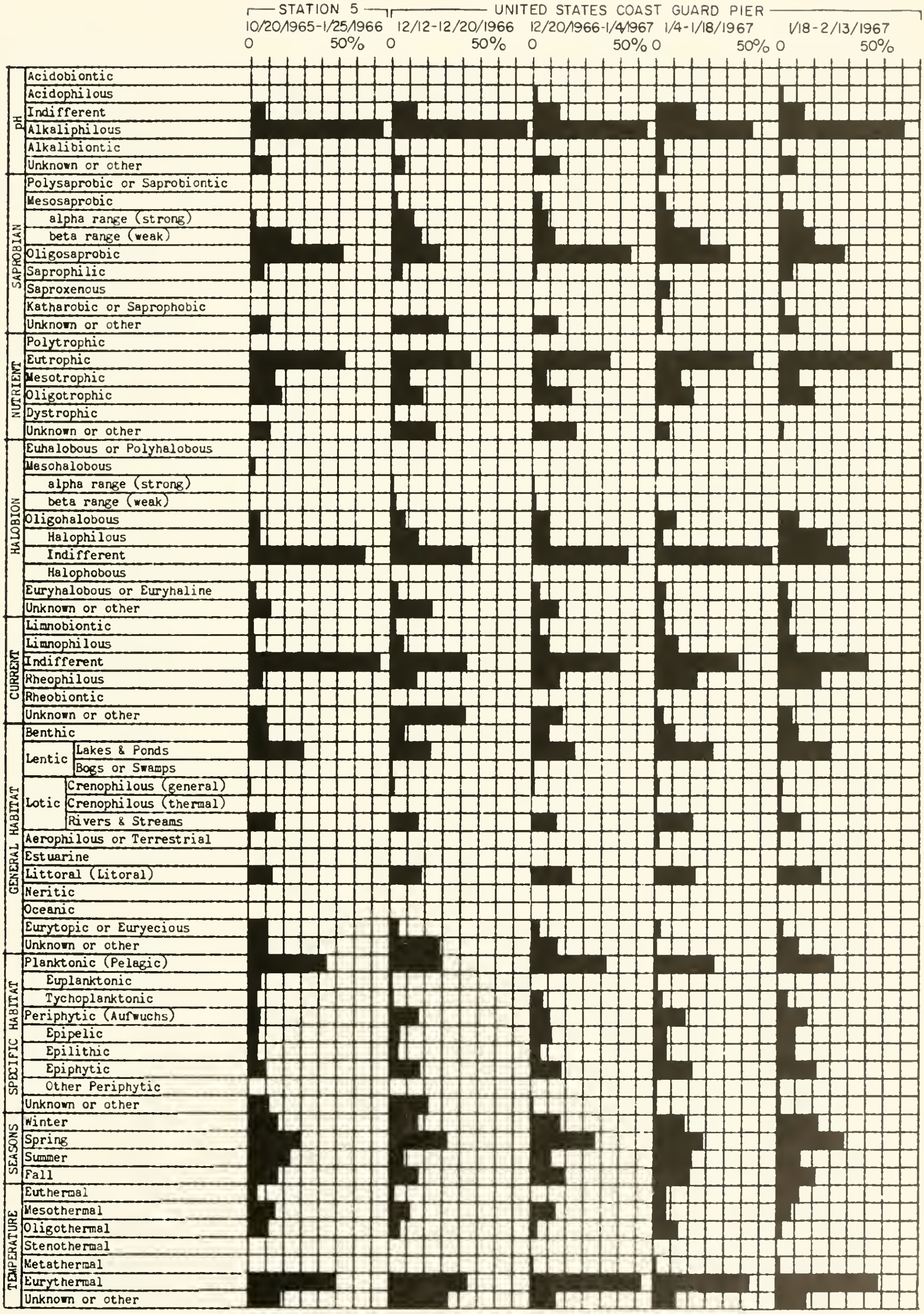

Fig. 2. Spectral histograms based on diatom species percentages from California-Nevada–FWPCA survey periphyton samples taken during intervals designated under each station.

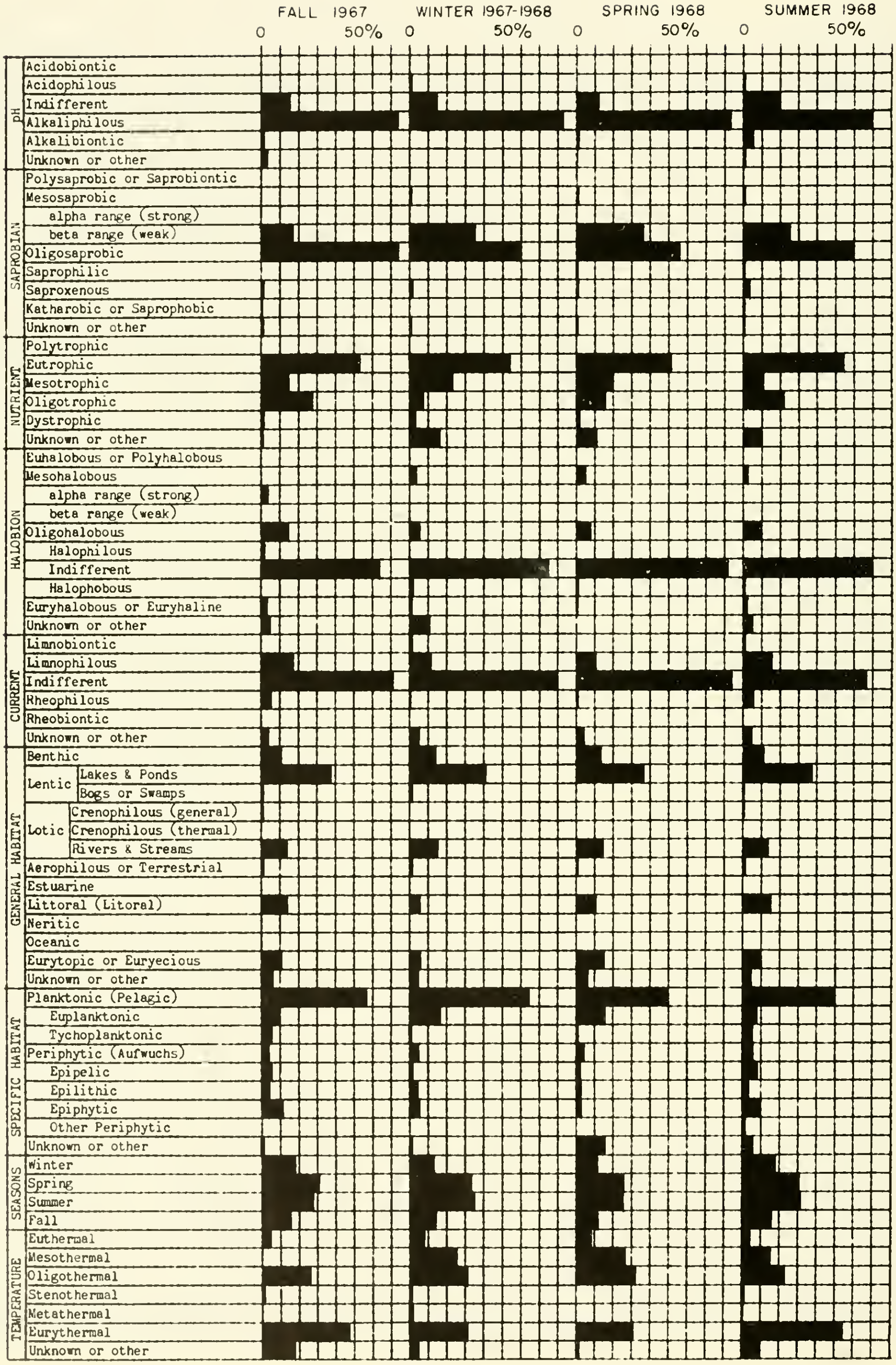

Fig. 3. Spectral histograms of diatom species percentages from averages of 15 fall 1967, 10 winter 1967–1968, 13 spring 1968, and 13 summer 1968 plankton samples at index station (Tahoe Pines) of Goldman (1974).

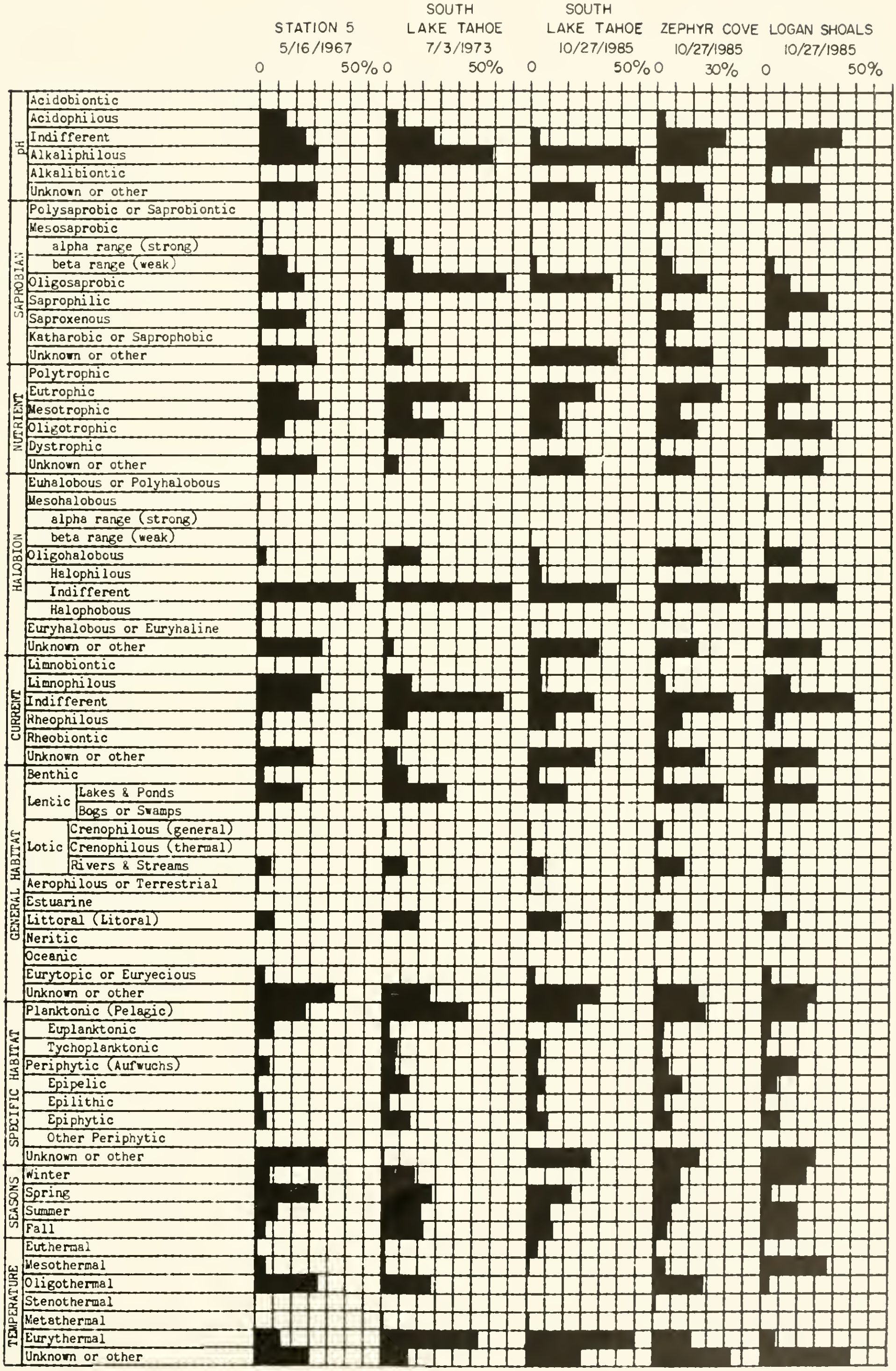

Fig. 4. Spectral histograms of diatom species percentages from the VanLandingham survey of 1967–1985; all stations were planktonic except Logan Shoals, which was periphytonic.

1974). One of the advantages of a comprehensive algal data synthesis like CAESARS is that the general and specific habitat spectra in conjunction with the nutrient and saprobian spectra can be helpful in determining if an alga is absent from an assemblage because of lack of suitable physical habitat or because of adverse water chemistry. Any artificial, comprehensive system of data synthesis involving the classification of ecological tendencies of algae is bound to have conspicuous deficiencies. Stoermer (1984) presents an excellent and objective discussion of some of these difficulties.

SAMPLES

California-Nevada–FWPCA Survey

PLANKTON.—Plankton grab samples were taken during this cooperative investigation from the following five stations on 27–30 April, 17–19 August, 28–30 September 1965; 25–27 January, 27–29 April, 16–18 August, 14–17 November 1966; and 6–8 February 1967 (California Department of Water Resources 1966, 1967). Histograms were made from diatom species percentages for the 6–8 February 1967 samples (Fig. 1).

Station 1 is about 1 km north of the mouth of the Upper Truckee River and at the edge of the southerly shelf of Lake Tahoe, El Dorado Co., California. The station is representative of conditions in shallower waters near an extensively developed residential and resort area and is responsive to surface inflow from tributary streams. Bottom depth is 7.5 m. Magnetic bearings from Station 1 are N 4° E to Cave Rock and S 86° E to the building on Globin's Pier at Al Tahoe (Fig. 5).

Station 2 is about 1.3 km northeast of the buoy at the mouth of Emerald Bay in El Dorado Co., California. The station is representative of conditions in deep waters and may be affected by inflows through Emerald Bay. Bottom depth is 345 m. Magnetic bearings from station are S 30° W to buoy "2" at the mouth of Emerald Bay and S 86° E to the building at Globin's Pier in Al Tahoe (Fig. 5).

Station 3 is 8.5 km south of Stateline Point and due west from Secret Harbor. The station is representative of waters in the deepest part of the lake and is at the eastern boundary of Placer Co., California. Bottom depth is 471 m. Magnetic bearings from Station 3 are N 8° W to Cal-Neva Lodge and S 67° W to Deadman Point on the Nevada shore (Fig. 5).

Station 3A (alternate station) is 5 km southwest of South Point, near the confluence of the Placer-El Dorado county line (California) with the Nevada state boundary. The station is representative of waters in the deepest part of the lake. Bottom depth is 465 m. Magnetic bearings from Station 3A are N 15° W to Cal-Neva Lodge and S 64° E to the Sahara Hotel at Stateline (Fig. 5).

Station 4 is 180 m from shore at a point 1.3 km west of Incline Creek, Washoe Co., Nevada. The station is representative of shallow waters in Crystal Bay and is responsive to inflow from Incline Creek. Bottom depth is 6 m (Fig. 5).

Station 5 is 1.3 km easterly from the dam at the lake outlet on the Truckee River at Tahoe City, Placer Co., California. The station is representative of shallow waters at the northwest corner of the lake and of the water flowing out of the lake. Bottom depth is 9 m. Magnetic bearings from Station 3 are N 38° W to the Chevron sign at Tahoe City Boat Works and N 20° E to the United States Coast Guard radio tower (Fig. 5).

PERIPHYTON.—Station 5 also was used for periphyton sampling. The bottom sample from this station, representing 20 October 1965–25 January 1968, was selected for comparison with four surface periphyton samples that were taken from the pier at the United States Coast Guard Station (2.9 km northeast of Tahoe City) at Lake Forest, Placer Co., California. Surface samples represented the time intervals of 2–20 December 1966, 20 December 1966–4 January 1967, 4–12 January 1967, and 18 January–13 February 1967. Spectral histograms were compiled from diatom species proportional counts from these five periphyton samples (Fig. 2). Permanent hyrax slides of both periphyton and planktonic samples from the stations mentioned above have been deposited at the United States National Museum of Natural History, Washington, D.C.

Goldman (1974) Survey

PLANKTON.—In Goldman's (1974) comprehensive study of the eutrophication of Lake Tahoe from 1967 through 1971, samples were taken on 115 different days from the designated index station at Tahoe Pines (in the Blackwood Creek–Madden Creek interfluve

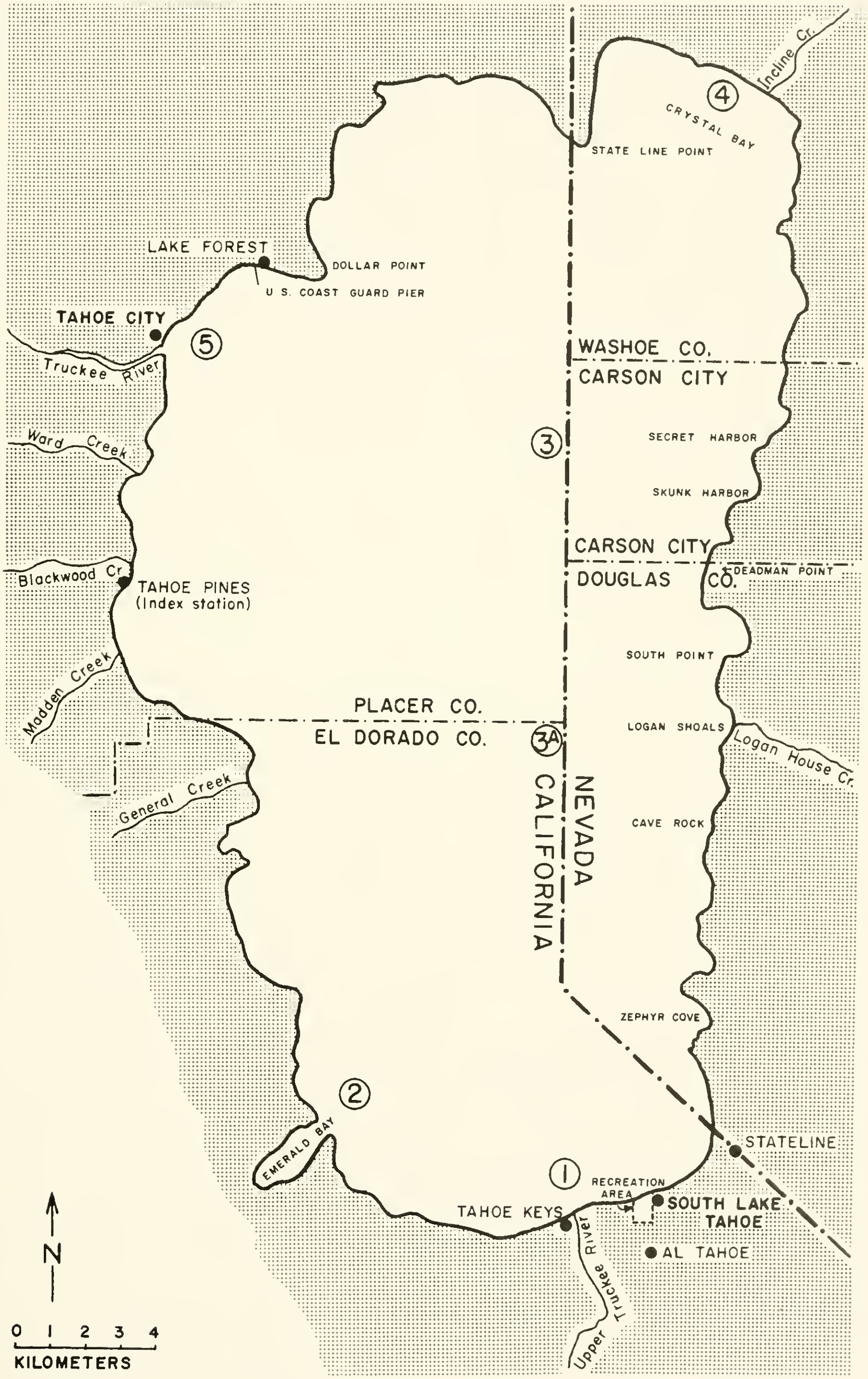
④
CRYSTAL BAY
Incline Cr.
STATE LINE POINT
LAKE FOREST
DOLLAR POINT
U. S. COAST GUARD PIER
TAHOE CITY
⑤
Truckee River
WASHOE CO.
CARSON CITY
③
SECRET HARBOR
SKUNK HARBOR
Ward Creek
CARSON CITY
DOUGLAS CO.
DEADMAN POINT
Blackwood Cr.
TAHOE PINES
(Index station)
SOUTH POINT
Madden Creek
PLACER CO.
EL DORADO CO.
3A
LOGAN SHOALS
Logan House Cr.
General Creek
NEVADA
CALIFORNIA
CAVE ROCK
ZEPHYR COVE
②
EMERALD BAY
STATELINE
①
RECREATION AREA
SOUTH LAKE TAHOE
TAHOE KEYS
AL TAHOE
Upper Truckee River
N
0 1 2 3 4
KILOMETERS

Fig. 5. Map of Lake Tahoe showing sites mentioned in this paper. Circled numbers represent sample stations of the California-Nevada–FWPCA survey.

area, Placer Co., California) (Fig. 5). Appendix C of that publication gave a tabulation of the average number of individuals (cells/ml) of each phytoplankton species for the entire 105-m water column at this station. The fall 1967 through summer 1968 sequence, represented by 51 sampling days, was used for plotting histograms (Fig. 3). Results from fall 1968 through fall 1971 sequences of samples were very similar and therefore were not figured. The fall 1967 spectra were plotted by totaling the average number of individuals of each diatom species for the entire 105-m water column for the 15-day fall 1967 sequence and then calculating the percentage of each diatom species in the total diatom community for that season. In the same manner, spectral histograms were generated for the 10 samples from the winter of 1967–1968, the 13 samples from the spring of 1968, and the 13 samples from the summer of 1968 (Fig. 3).

PERIPHYTON.—Goldman (1974) showed the relative proportions of periphyton (mostly diatoms) for the intervals of 24 June–30 September 1970 and 1 October 1970–2 May 1971 from several stations around Lake Tahoe in the vicinity of the following localitites: General Creek, Emerald Bay, and Tahoe Keys in El Dorado Co., California; Zephyr Cove and Cave Rock in Douglas Co., Nevada; Skunk Harbor in Carson City, Nevada; Incline Creek and Crystal Bay in Washoe Co., Nevada; and Dollar Point (Lake Forest), Ward Creek, and Tahoe Pines in Placer Co., California (Fig. 5). These samples are discussed below under OBSERVATIONS.

VanLandingham Survey of 1967–1985

PLANKTON.—My own survey of the diatoms of Lake Tahoe began with plankton samples from Tahoe City (Station 5) on 28 March 1967 and continued with samples at irregular times from this and three other stations until 28 October 1985. Because of possible differences in species interpretations in the California-Nevada–FWPCA joint survey, several samples were sent to various investigators and laboratories for determinations, comparisons, and verifications. The Academy of Natural Sciences of Philadelphia laboratory and I examined the 16 May 1967 plankton sample from Station 5 (Fig. 4). Our species determinations were very similar. Permanent hyrax slides are deposited at the Geology Department, California Academy of Sciences, San Francisco. The samples were prepared for microscopic examination and species proportional analysis following VanLandingham (1976). Since July 1973, sampling has been restricted to three stations in the southeast portion of the lake:

Station A (South Lake Tahoe) is about 1 km west of the boat harbor near the South Lake Tahoe Recreation Area, El Dorado Co., California (Fig. 5). This station was chosen for its close proximity to the most densely populated and highly developed region of the lake. Spectral histogram results from two samples separated by a 12-year span from this station can be compared (Fig. 4).

Station B (Zephyr Cove) is 1.5 km northeast of Zephyr Point at the Zephyr Cove pier, Douglas Co., Nevada (Fig. 5). Although there are some recreational and commercial facilities in the area, it is not heavily populated. A series of histograms was plotted for the 27 October 1985 sample from this station (Fig. 4).

PERIPHYTON.—Station C (Logan Shoals) is 2.5 km north of Cave Rock and near the mouth of Logan House Creek in Douglas Co., Nevada (Fig. 5). This is one of the few remaining, relatively unspoiled areas on Lake Tahoe. It is the only station encountered in this study that I have found to be oligotrophic more often than mesotrophic and/or eutrophic on the basis of indicator algae. At this station periphyton was scraped at irregular intervals from plants and large boulders at the water's edge. The spectral histograms were composed for a recent sample from 27 October 1985 (Fig. 4).

OBSERVATIONS

California-Nevada–FWPCA Survey

PHYTOPLANKTON.—The 27–30 April 1965 and 25–27 January 1966 plankton diatoms from samples of the California-Nevada–FWPCA joint investigation indicated a pronounced mesotrophic character for the entire lake. The prominence of *Synedra nana* Meist., an indicator of mesotrophy (Cody 1978), was responsible for the strong mesotrophic nature of these samples. The remaining dominant species, all of which were eutrophic (and/or mesotrophic) indicators except *Cyclotella bodanica* Eul. *ex* Grun. and *Stephanodiscus invisitatus* Hohn & Hell., accounted for a less pronounced but conspicuous eutrophic character. The percentages of the most dominant species from the 27–30 April 1965 samples were as follows: Station 1, *Fragilaria crotonensis* 52, *Synedra nana* 21, *Stephanodiscus invisitatus* 4, and *Nitzschia acicularis* (Kütz.) W. Sm. 3; Station 2, *S. nana* 39, *Asterionella formosa* Hass. 29, *F. crotonensis* 20, and *N. acicularis* 6; Station 3, *F. crotonensis* 47, *S. nana* 37, *N. acicularis* 4, and *A. formosa* 3; Station 4, *S. nana* 31, *F. crotonensis* 30, *F. construens* (Ehr.) Grun. 3, and *Amphiprora (Entomoneis) paludosa* W. Sm. 3; and Station 5, *S. nana* 41, *N. acicularis* 11, and *F. crotonensis* 4. The dominant species from the 25–27 January 1966 samples were as follows: Station 1, *F. crotonensis* 48, *S. nana* 33, *F. construens* 4, and *Melosira italica* (Ehr.) Kütz. 4; Station 2, *S. nana* 53, *F. crotonensis* 15, *M. italica* 8, and *F. pinnata* 5; Station 3A, *S. nana* 59, *F. crotonensis* 21, *A. formosa* 6, and *N. acicularis* 3; Station 4, *F. crotonensis* 43, *S. ñana* 35, *F. construens* 6, and *A. formosa* 5; and Station 5, *F. crotonensis* 48, *S. nana* 23, *C. bodanica* 8, and *M. italica* 3. Eutrophic and/or meso-trophic diatoms prevailed at all five stations in the plankton samples collected on 17–19 August and 28–30 September 1965. Only Sta-tion 2 (at the August sampling) showed any marked tendency toward oligotrophy.

A similar trend toward mesotrophy in the winter can be seen in the first three stations on 6–8 February 1967 (see nutrient spectrum, Fig. 1). Station 4 (Fig. 1) was anomalous and showed an oligotrophic nature that was found rarely in the plankton. In all of these samples *Cyclotella bodanica* was dominant, but *Synedra nana*, *Fragilaria crotonensis*, and many other mesotrophic and eutrophic indicators were important. The nutrient spectra of all stations (Fig. 1) correlate well with both the saprobian and pH spectra. Mesotrophic waters usually are concomitant with oligosaprobic and/or saproxenous conditions in the saprobian spectrum and with indifference in the pH spectrum. Oligohalobous indifference in the halobion spectrum is to be expected in subalpine lakes. The prominent limnophilous element in the current spectrum and the prominent lake and pond category in the general habitat spectrum suggest that the plankton at this time of the year is mostly indigenous to the lake and not carried in from streams. The specific habitat spectrum confirmed the planktonic nature of the samples. Because the seasonal distribution of most of these planktonic diatoms is imperfectly known, the seasonal spectrum gave inconclusive results. VanLandingham (1964) and others have pointed out that temperature and nutrients are more important in diatom distribution than seasonal influence. The strong oligothermal character of the temperature spectrum is normal and reflects the cold-water characteristics which would be expected in the plankton of a large, subalpine lake in the winter. On the other hand, samples from all of the periphyton stations from cold times of the year (late fall–winter) were eurythermal (widely tolerant of temperature changes) (Fig. 2).

Eutrophy in the nutrient spectrum normally is correlative with oligosaprobic to weak mesosaprobic conditions in the saprobian spectrum and with alkaliphilous conditions in the pH spectrum. Spring plankton samples of 27–29 April 1966 demonstrated this very well as did periphyton samples (Fig. 2) and the Tahoe Pines plankton samples (Fig. 3). *Fragilaria crotonensis* was the most abundant diatom at all stations (composing 98% of the assemblage at Station 2) in the 27–29 April 1966 plankton samples. Although *F. crotonensis* was less important (becoming more subordinant to *Fragilaria construens* and *F. pinnata*) in the summer (16–18 August) samples and the fall (14–17 November) samples, the conspicuous eutrophic conditions remained. A sample from a depth of 25 m was taken at Station 2 in the summer to supplement the regular 3-m sample from that station. The two most dominant diatoms, *Cyclotella meneghiniana* Kütz. and *C. atomus* Hust., from the deep sample were prominent eutrophic indicators and accounted for 39% and 30%, respectively, of the total diatom community.

Periphyton.—It is noteworthy that the mesotrophic trend found in diatoms of the plankton samples of 6–8 February 1967 (Fig. 1), 25–27 January 1968, and 27–30 April 1965 did not occur in any of the periphyton samples (Fig. 2). *Fragilaria construens*, *F. pinnata*, *Synedra vaucheriae* Kütz., and *Nitzschia kuetzingiana* Hilse (all of which are characteristic of eutrophic waters) accounted for most of the prominent eutrophic aspect of all of these periphyton samples; the last of these species is a diagnostic eutrophic indicator (Krieger 1927, Jørgensen 1948, Cleve-Euler 1953, Kolbe 1953, Van der Werff and Huls 1957–1974, Cholnoky 1968, Schoeman 1973, Moghadam 1976, Caljon 1983). In large lakes it is not unusual to find planktonic taxa composing a large part of the periphyton assemblages, hence the large proportion of plankton in the specific habitat spectrum of all the periphyton samples (Fig. 2). This phenomenon also can be seen in the specific habitat spectrum of the Logan Shoals periphyton sample of the VanLandingham survey (Fig. 4).

Goldman (1974) Survey

PHYTOPLANKTON.—Goldman (1974) stated in his conclusions,

> *Cyclotella bodanica* and *Melosira crenulata* are dominant centric diatoms while *Fragilaria crotonensis* is the most important pennate. These three oligotrophic forms account for about 80% of the phytoplankton biomass throughout the year.

It is likely that only one of these, *C. bodanica*, is an oligotrophic form (Hustedt 1930, Van der Werff and Huls 1957–1974, Tamás 1964, Hutchinson 1967, Duthie and Sreenivasa 1971, Sreenivasa and Duthie 1973, Almer et al. 1974, Rosén 1981). However, there are many reports of it in eutrophic or mesotrophic waters, such as Lipscomb (1966). On the other hand, Hillard (1959) noted that a slight pulse in *C. bodanica* corresponded with eutrophy. Recent taxonomic research suggests that *C. bodanica* may grade into *C. comta* Fricke. The report on centric diatoms of Lake Tahoe by Mahood et al. (1984) discussed *C. comta* in detail but did not mention *C. bodanica*. There is no clear consensus in the numerous references in CAESARS that shows *C. comta* to be correlative with any particular trophic status. It is probably eurytrophic (indifferent to inorganic nutrient content).

Melosira crenulata is a junior synonym of *M. italica*, which most authorities consider to be a eutrophic indicator. Mahood et al. (1984) state that *M. italica* is alkaliphilous and mesotrophic. Reynolds (1984) is one of the few references that gives it a distinct mesotrophic designation. Although Van der Werff and Huls (1957–1974) and Bradbury (1972a) indicated that *M. italica* is mesotrophic, they also implied that its range extended into the oligotrophic and/or eutrophic zones. However, if it is indeed mesotrophic, the probability of its being alkaliphilous is subject to serious question. It is more likely that it is not mesotrophic but alkaliphilous and eutrophic. If there is any propensity for mesotrophic diatoms to correlate with a position in the pH spectrum, it is with indifference (occurrence around pH 7), which is to be expected if one follows the explanations of Fjerdingstad (1965a), Sparling and Nalewajko (1970), and VanLandingham (1976). Although there have been indications that *M. italica* may be acidophilous (Niessen 1956, Round 1961), 17 CAESARS references categorize it as alkaliphilous (Foged 1958, 1959, 1976, 1980a, Maillard 1959, Liebmann 1962, Cholnoky 1968, 1970a, VanLandingham 1970, Ehrlich 1973, Gasse 1975, Kaczmarska 1976, Řeháková 1976, Moreira and Moreira 1982, 1984, Gasse and Tekaia 1983, Dixit and Dickman 1986; 4 as alkaliphilous to indifferent (Hustedt 1957, Gasse 1972, Lowe 1974, Foged 1978); and 8 as indifferent (Foged 1954, 1957, 1970, Haworth 1969, Messina-Allen and VanLandingham 1970, Baudrimont 1974, Khursevich 1976, Del Prete and Schofield 1981). If *M. italica* is conceded to be alkaliphilous, it is much more likely to have the associated eutrophic correlation found with over 100 commonly occurring diatoms. Only Round (1960), Cholnoky (1970a), Stockner (1971), and Weber (1973) indicated that *M. italica* might be characteristic of oligotrophic waters, while there is much more agreement concerning its correlation with eutrophic waters (Krieger 1927, Hustedt 1930, 1942, Brockmann 1935, Frenguelli and Cordini 1937, Foged 1951, 1959, Bourrelly and Manguin 1952, Järnefelt 1952, Guermeur 1954, Messina-Allen and VanLandingham 1970, VanLandingham 1970, Baudrimont 1974, Planas 1975, Gasse 1975, and Negoro 1981). Mesohalobous (characterized by brackish water, 0.5–3.0% salt) organisms are very rare in alpine and subalpine lakes. The statement of Mahood et al. (1984) that *M. italica* is mesohalobous seems doubtful in view of the evidence that only Van der Werff and Huls (1957–1974) reported it from the weak mesahalobous zone (but also in the oligohalobous zone). If *M. italica* is truly mesohalobous, why would it be so common in a high, subalpine lake, such as Lake Tahoe? There is even some consensus that *M. italica* has a negative correlation with salt content since Cleve-Euler

(1951), Hustedt (1957), Palik (1958), and Baudrimont (1974) regarded it as halophobous (salt-deficient waters) and Gasse (1972), Lowe (1974), and Řeháková (1976) as halophobous to indifferent. However, the greatest consensus is that it is oligohalobous (indifferent): Kolbe (1927, 1953), Cholnoky (1929), Brockmann (1954), Foged (1954, 1957, 1959, 1970, 1976, 1978, 1980a, 1982), Messina-Allen and VanLandingham (1970), VanLandingham (1970), Gasse (1975), Khursevich (1976), and Moreira and Moreira (1982).

In the examination of over 4,000 references, no indication was found that *Fragilaria crotonensis* was clearly diagnostic of oligotrophic waters, although it is sometimes found in large numbers in those waters. Beeton (1965), Stoermer and Yang (1970), Stoermer et al. (1974), Stoermer and Ladewski (1976), and Grimes et al. (1984) suggested that it ranged from oligotrophic to eutrophic. Van der Werff and Huls (1957–1974) gave a dystrophic to eutrophic (and/or hypertrophic) range. Teiling (1955), Rawson (1956), Patrick and Reimer (1966), Tarapchak and Stoermer (1976), and Gerrath et al. (1980) considered it to be most prominent in mesotrophic waters. It has been described as mesotrophic-eutrophic by Cleve-Euler (1953), Round and Brook (1959), and Lowe (1974). But the greatest agreement is in favor of its eutrophic tendency: Krieger (1927), Hustedt (1930), Jørgensen (1948), Margalef (1957), Hutchinson (1967), Stockner and Benson (1967), Lehn (1969), Frey (1969), Vollenweider (1970), Stockner (1971), Stoermer et al. (1971), Stadelmann (1971), Bradbury (1972a, 1972b), Haworth (1972a), Nikaloyev and Petrova (1978), Burns and Mitchell (1974), Planas (1975), Gorham and Sanger (1976), Holtan (1978), Bailey and Davis (1978), Cassie (1979), Cassie and Freeman (1980), Rosén (1981), Negoro (1981), Mason (1981), Brugam and Patterson (1983), Reynolds (1984), Haffner et al. (1984), and Engstrom et al. (1985). In addition, Stockner (1972) stated that it correlates well with domestic sewage discharge into lakes. Stoermer et al. (1974) and Bradbury (1975) advocate that it is eurytopic, as do Duthie and Sreenivasa (1971), but with acknowledgment of its eutrophic character. *Fragilaria crotonensis* requires for optimal growth more than 20 μg P l^{-1} (Fogg 1973). Løvstad (1984) indicated a sharp drop in the development of *F. crotonensis* at concentrations of less than 16 μg P l^{-1} in eutrophic Lake Jaren in April and May 1976. Goldman (1974: 72) stated that *F. crotonensis* "is now the dominant type in Lake Tahoe, both in biomass and numbers." Such a diatom (which, according to 21 references supplied by CAESARS, is found only in the oligosaprobic and/or weak mesosaprobic zones) seems out of place in such large numbers in a body of water so oligotrophic as Lake Tahoe is alleged to be.

It is known that *F. crotonensis* has a pronounced correlation with alkaliphilous conditions (optimum development above pH 7) (Jørgensen 1948, Foged 1948, 1953, 1954, 1958, 1959, 1968, 1969, 1970, 1978, 1980a, 1980b, 1982, Hustedt 1957, Van der Werff and Huls 1957–1974, Round 1964, Patrick et al. 1968, Cholnoky 1968, Stoermer et al. 1971, Besch et al. 1972, Del Prete and Schofield 1981, Brugam and Patterson 1983, and Dixit and Dickman 1986). Fjerdingstad (1965a), Sparling and Nalewajko (1970), and VanLandingham (1976, 1982), among many others, have pointed out that definite correlations can be made between trophic status of lakes and their pH: eutrophic habitats generally correspond with a high pH (above 7), mesotrophic habitats generally correspond with an intermediate or circumneutral pH, and oligotrophic habitats generally correspond with a low pH (below 7). Studies from 1951 to 1967 showed pH values from the lake to be invariably above 7, in one instance reaching a maximum of 8.4 (California Department of Water Resources 1967). None of the samples examined in my study of 1967–1985 ever had a pH below 7.2.

According to Goldman (1974: 131), the five most dominant species of phytoplankton at the index station (Tahoe Pines) for 1967–1969 (in order of importance) were *Fragilaria crotonensis*, *Melosira crenulata* (=*M. italica*), *Fragilaria pinnata*, *Stephanodiscus astraea* (Ehr.) Grun., and *Cyclotella bodanica*. Although the trophic disposition of *F. pinnata* is considered to be oligotrophic or mesotrophic through eutrophic (Van der Werff and Huls 1957–1974, Stoermer et al. 1971) and oligotrophic (Beeton 1965, Baudrimont 1974), the greatest number of authorities deem it to be eutrophic (Hustedt 1937, 1938, Jørgensen 1948, Foged 1951, 1959, Bourrelly and Manguin 1952, Ross 1952, Cleve-Euler 1953, Messina-Allen and VanLandingham 1970, VanLandingham 1970, Gasse 1972, 1974a, 1974b, Lowe 1974, and Caljon 1983).

Stephanodiscus astraea and its varieties are some of the most diagnostic of all indicators of eutrophy. According to CAESARS, apparently no authorities judge *S. astraea* to be exclusively oligotrophic. Cleve-Euler (1951), Patrick (1956), and Werff and Huls (1957–1974) consider the trophic range to be oligotrophic and/or mesotrophic through eutrophic, but most investigators agree that it is eutrophic (Krieger 1927, Hustedt 1930, 1942, 1949, Jørgensen 1948, Foged 1948, 1951, 1953, 1959, Bourrelly and Manguin 1952, Kolbe 1953, Guermer 1954, Brockmann 1954, Round and Brook 1959, Hutchinson 1967, Gasse 1969, 1972, 1974b, 1975, Haworth 1972b, Moreira 1975, Stoermer and Ladewski 1976, and Mason 1981). Mahood et al. (1984) did not mention *S. astraea* but did comment on *Stephanodiscus alpinus* Hust., a closely related form. It is highly unlikely that *S. alpinus* is alkalibiontic, as they claim. Alkalibiontic species are rare among the diatoms. Out of a total of 2,900 diatom taxa, CAESARS reveals that no more than two dozen are definite alkalibionts, none of which are centrics except *Stephanodiscus dubius* (Fricke) Hust. *Stephanodiscus alpinus* may be eutrophic as Hohn (1969) and Mahood et al. (1984) imply. However, Ayers et al. (1967) indicate that it might be oligotrophic, and Tarapchak and Stoermer (1976) note maximum abundance in the mesotrophic zone. Although it occurs in very oligotrophic lakes, it seems to become more abundant with moderate degrees of eutrophication (Stoermer 1978, Håkansson and Stoermer 1984).

Goldman (1974: appendix) shows very conspicuous pulses of *Synedra radians* Kütz. (= *Synedra acus* var. *radians*) at the index station in summer 1969, spring 1970, and winter, spring, and fall 1971. Apparently only Whitford and Kim (1971) found *S. radians* to be oligotrophic. It is thought to be mesotrophic (Ayers et al. 1967), mesotrophic through eutrophic (Cleve-Euler 1953, Van der Werff and Huls 1957–1974), and eutrophic (Jørgensen 1948, Lowe 1974).

According to Goldman (1974), on 13 May 1970 *Microcystis (Polycystis) aeruginosa* Kütz. had a total of 5.76 individuals/ml for the entire 105-m water column at Tahoe Pines. At that time, *M. aeruginosa* composed 5.1% of the total phytoplankton population and was outnumbered only by the diatoms *Melosira italica* (=*M. crenulata*), *Asterionella formosa*, and *Fragilaria crotonensis*. Evidently there are no reports of *M. aeruginosa* being found exclusively in oligotrophic waters. It is well known as a waterbloom-forming blue-green alga. Although there are sporadic reports of this taxon on certain occasions from mesotrophic waters (Mabille 1956, Rawson 1956), it nearly always is found in close correlation with eutrophic and/or mesotrophic waters (Krieger 1927, Redeke 1935, Nygaard 1949, Fjerdingstad 1950, Gerloff et al. 1952, Järnefelt 1952, Teiling 1955, Round and Brook 1959, Prescott 1962, Lund 1962, Beeton 1965, Cairns et al. 1972, Peelen 1975, Nikolayev and Petrova 1978, Hickman 1979, Cassie and Freeman 1980, Parra et al. 1980, Takahashi et al. 1981, Rosén 1981, Okada et al. 1981, Coard et al. 1983, Nicklisch and Kohl 1983, Caljon 1983, Cáceres and Reynolds 1984, Takamura and Yasuno 1984, Reynolds 1984).

Dinobryon sertularia Ehr. made up a considerable portion of the total algae community on at least three occasions at Tahoe Pines, having a total of 38.34, 18.99, and 21.42 individuals/ml for the entire 105-m water column on 9 and 16 May 1968 and 24 July 1969, respectively (Goldman 1974). On these three occasions, *D. sertularia* was an important subdominant, composing 18, 10, and 28.8%, respectively, of the total population. In the same publication (Goldman 1974: Fig. 2), apparently *D. sertularia* is referred to as *Dinobryon sociale* Ehr. Both of these taxa are eutrophic. Such investigators as Krieger (1927), Huber-Pestalozzi (1941), Meyer and Brook (1969), and Gerrath et al. (1980) believe that *D. sertularia* occurs under eutrophic conditions, while Krieger (1927) and Huber-Pestalozzi (1941) hold the same opinion for *D. sociale*.

Sphaerocystis schroeteri Chod. was the dominant algal species on nine different occasions in the fall of 1967 at the Tahoe Pines station (Goldman 1974). In spite of the fact that it is occasionally found in oligotrophic lakes (Almer et al. 1974), many such writers as Meyers and Brook (1968) describe *S. schroeteri* as eutrophic, whereas Reynolds (1984) contends that it is mesotrophic.

There is good evidence that in some areas of Lake Tahoe the algae display an oligotrophic tendency at certain times. Goldman (1974: 131) found *Cyclotalla stelligera* to be uncommon at the index station (Tahoe Pines) in 1967–1971 but to be present in large numbers in midlake plankton samples in 1972–1973. CAESARS provides a strong opinion that *C. stelligera* is typical of oligotrophic waters: Jørgensen (1948), Cleve-Euler (1951), Hutchinson (1967). Stockner (1971), Schnitzler (1971), Holland and Beeton (1972), Croome and Tyler (1973), Burns and Mitchell (1974), Lowe (1976), Bailey and Davis (1978), Cassie and Freeman (1980), Smol et al. (1983), Schelske (1984), and Engstrom et al. (1985). Smedman (1969), Bradbury (1972b), and Tarapchak and Stoermer (1974) advocate dystrophic-oligotrophic, oligotrophic-mesotrophic, and mesotrophic categories, respectively, while Duthie and Sreenivasa (1971) suggest it is "eurytopic-eutrophic." Only Cholnoky (1968, 1970b), Lowe (1974), and Moghadam (1976) support the contention of Mahood et al. (1984) that it is eutrophic. Sewage export from the Tahoe basin in recent years may be responsible for the increase of such oligotrophic indicators as *C. stelligera* at various places in the lake. On the other hand, most of the evidence supplied by the VanLandingham survey of the years 1967–1985 suggests that the propensity toward mesotrophy (or even eutrophy) displayed by the most dominant diatoms is still strong over much of the lake.

Periphyton.—In spite of the fact that the littoral zone contributes a small portion of the total primary productivity and that the lake has great area and depth, the importance of the littoral areas and periphyton cannot be overlooked in a comprehensive evaluation of the lake's trophic characteristics. The seven most dominant species in the periphyton from 11 stations around Lake Tahoe between 1 October 1970 and 2 May 1971 were: *Synedra actinastroides* Lemm., *Fragilaria crotonensis*, *Gomphonema parvulum* Kütz., *Cyclotella bodanica*, *Synedra ulna*, *Gomphoneis herculeana* (Ehr.) Cl., and *Melosira crenulata* (Goldman 1974: Fig. 55). CAESARS indicates that only *C. bodanica* is predominantly oligotrophic; all of the rest are eutrophic, except *G. herculeana*. The six most important diatoms in the periphyton from 10 stations around Lake Tahoe between 24 June and 30 September 1970 were: *Epithemia argus* (Ehr.) Kütz., *Rhopalodia gibba* (Ehr.) O. Müll., *Synedra ulna*, *Cymbella ventricosa* Ag., *Navicula aurora* Sov., and *Fragilaria capucina* Désm., none of which clearly indicates oligotrophic conditions and most of which are eutrophic indicators. Goldman (1974) notes that *F. capucina* was a dominant species in the periphyton of the summer of 1971 only off the Upper Truckee River mouth and in Emerald Bay, both of which are noted for high productivity. Many authorities think that *F. capucina* is a good enrichment indicator. However, Schröder (1939) states that it is not particularly sensitive to pollution. Only Rawson (1956) and Beeton (1965) place it directly in the oligotrophic zone. Cleve-Euler (1953) and Van der Werff and Huls (1957–1974) assign it to the dystrophic through mesotrophic and/or eutrophic zones. The range given by Round and Brook (1959) is mesotrophic-eutrophic. However, nearly all authorities regarded it as eutrophic: Krieger (1927), Hustedt (1930, 1938, 1942), Jørgensen (1948), Foged (1951, 1959), Bourrelly and Manguin (1952), Holland (1965), Gasse (1969), Bradbury (1972b), Stoermer et al. (1974), Lowe (1974), Stoermer and Ladewski (1976), Tarapchak and Stoermer (1976), and Bailey and Davis (1978).

VanLandingham Survey of 1967–1985

Phytoplankton.—Many of my own samples from Tahoe City (station 5 of the California-Nevada–FWPCA survey) demonstrated marked fluctuations in the histograms of all spectra at different times of the year. However, mesotrophic and/or eutrophic conditions always predominated in the nutrient spectrum. In the 16 May 1967 plankton sample from station 5 (Fig. 4), *Synedra nana* (25% of the total) was responsible for most of the mesotrophic manifestation, and *Fragilaria crotonensis* (20% of the total) accounted for most of the eutrophic manifestation. This sample, which comes from the northeastern portion of the lake, is included for comparison with samples from the three stations (South Lake Tahoe, Zephyr Cove, and Logan Shoals) in the southeastern portion of the lake and with other results from station 5 (Figs. 1–2). Spectral histograms of diatom species percentages from plankton samples at the South

Lake Tahoe station on 3 July 1973 and 27 October 1985 can be compared in Figure 4. Other samples were taken at South Lake Tahoe during the long interval represented by these two samples, but their histograms were not figured because of their great similarities. After a period of over 12 years, one can see the similarity of the spectra in these two samples and the eutrophic aspects of both. The diminishing of the eutrophic category in the 1985 sample in relation to the 1973 sample may be a result of sewage export from the Tahoe basin in recent years. The planktonic assemblage from Zephyr Cove on 27 October 1985 was very typical of that station and exhibited the usual eutrophic characteristics (Fig. 4); counts for the diatoms were about 20 cells/ml. *Cyclotella glomerata* Bach., *Achnanthes lanceolata, Nitzschia linearis* (Ag.) W. Sm., and *Cocconeis diminuta* Pant. were the dominant taxa, the last of which is a diagnostic mesotrophic to eutrophic indicator (Hustedt 1938, Jørgensen 1948, Cleve-Euler 1953, Foged 1957).

PERIPHYTON.—After studying hundreds of samples over a period of 18 years from many stations in the three independent surveys of Lake Tahoe, I have found Logan Shoals to be the only station (planktonic or periphytonic) in which the indicator algae suggest general oligotrophic conditions more often than mesotrophic and/or eutrophic (Fig. 4).

CONCLUSIONS

The slight increase in recent years in oligotrophic algae, such as *Cyclotella stelligera* and *Achnanthes minutissima*, and the corresponding slight decrease in the dominant mesotrophic and eutrophic algae at various places in the lake seem to correlate well with the export of sewage from the Tahoe basin. This situation bears testimony to the sensitivity of the algae as indicators. However, the strong mesotrophic-eutrophic trend, which was indicated by the algae from about 1965 until about 1973 or 1974, still continues today, although probably to a lesser degree. Moreover, repeated spills of raw and partially treated sewage have been indicated adequately by the microalgae populations and other modes of observation to such an extent that the United States Environmental Protection Agency and California's regional water quality control board have duly noted that the Lake Tahoe water reuse system for recycling sewage into drinking water is no longer feasible (U.S. Water News 1986). It could be claimed that the persistence and prominence of a whole suite of characteristically eutrophic (and/or mesotrophic) diatoms in a lake traditionally thought to be oligotrophic attests to the admonition that we should reexamine either the lake or the validity of the algal indicator concept (or both). Can algal communities be valid indicators of the trophic status of a lake or do physical and chemical factors provide the only reliable clues to deciphering trophic status? If the former is true, then our traditional opinions about Lake Tahoe will have to change. If the latter is true, then there should be dynamic changes in limnological thought. In either case, it seems prudent to maintain philosophical objectivity and consider all aspects of biological, physical, and chemical factors in trophic assessment, even if they seem to be contradictory. If it is granted that Lake Tahoe is not highly anomalous, then undoubtedly it is somewhat less "ultra-oligotrophic" than the water chemists and physical limnologists would advocate, and probably the indicative diatoms and other algae are somewhat less accurate than the diatomists and aquatic biologists would advocate.

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ZONATION PATTERNS IN THE VASCULAR PLANT COMMUNITIES OF BENTON HOT SPRINGS, MONO COUNTY, CALIFORNIA

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ABSTRACT.—Vascular plant communities surrounding Benton Hot Springs, Mono County, California, were studied. The springs complex is comprised of two thermal springs, a thermal stream, and a cooling pond. Water temperatures varied from 57 C in one hot spring to 45 C at the cooling pond. The vegetation showed concentric zones about the springs and cooling pond and parallel zones beside the stream. Each zone demonstrated its own dominant plant species with some species being present in two or more zones. A total of six zones were identified plus an algal mat on the springs themselves. Soil factor patterns varied from spring to desert as did vegetational parameters. Soil moisture appeared responsible for most of the patterns observed.

Thermal springs are common throughout western North America. They occur in a variety of elevations and habitat types and are popular sites for recreation. The waters of thermal systems vary widely in temperature and mineral content (Loam 1980). It is common for such springs to contain high levels of dissolved minerals, some of which should exert influence on the surrounding vegetation.

The ecology of vascular plant communities surrounding thermal springs is not well known. Meadow vegetation surrounding warm springs in the Great Basin of western North America has been described by Bolan (1964). Bolan studied vegetation surrounding springs at Fish Springs National Wildlife Refuge, Tooele County, Utah, where he discussed 10 community types. The zonation patterns surrounding these springs were predominantly influenced by soil salinity.

Ranwell (1973) stated that soil structure, soil particle size, and soil moisture were important factors in determining growth and zonation of vascular plants in marsh habitats. In addition, Skougard and Brotherson (1979) discussed the influence of soil moisture, pH, and soluble salts on several distinct vegetation zones in playa meadows in central Utah. They found that salinity had the greatest influence on community structure, followed by soil moisture.

Shupe et al. (1986) examined the vegetation patterns surrounding several cold springs in Utah County, Utah. These authors found that soil moisture and salinity largely accounted for the observed patterns. As distance from the springs increased, salt levels in the soil increased and soil moisture decreased. Halophytic species generally increased with distance from the spring sources.

Literature treating the ecology of meadow vegetation arising from thermal springs is nearly absent. This paper attempts to add information to our knowledge of these interesting and distinct ecosystems by describing the vegetative zonation patterns surrounding hot springs near Benton, Mono County, California (Fig. 1).

STUDY SITE

The Benton thermal area is comprised of two thermal springs, a thermal stream, and a cooling pond. The first spring is hot, with water at 57 C. This spring, approximately 3 m in diameter, is drained by a stream flowing at an initial temperature of 57 C that cools to 45 C at the cooling pond. Following cooling, the water is used for irrigation. The second spring is cooler and larger, with a temperature of 33 C and a diameter of 10 m. This spring also drains into the stream.

The thermal complex at Benton is surrounded by a meadow with well-developed zonation patterns. Vegetation surrounding the hot spring occurs in two major zones. Zonation patterns around the warm spring, stream, and cooling pond are more extensive, with four zones evident. In addition to the zonation evident in the vascular plants, all of

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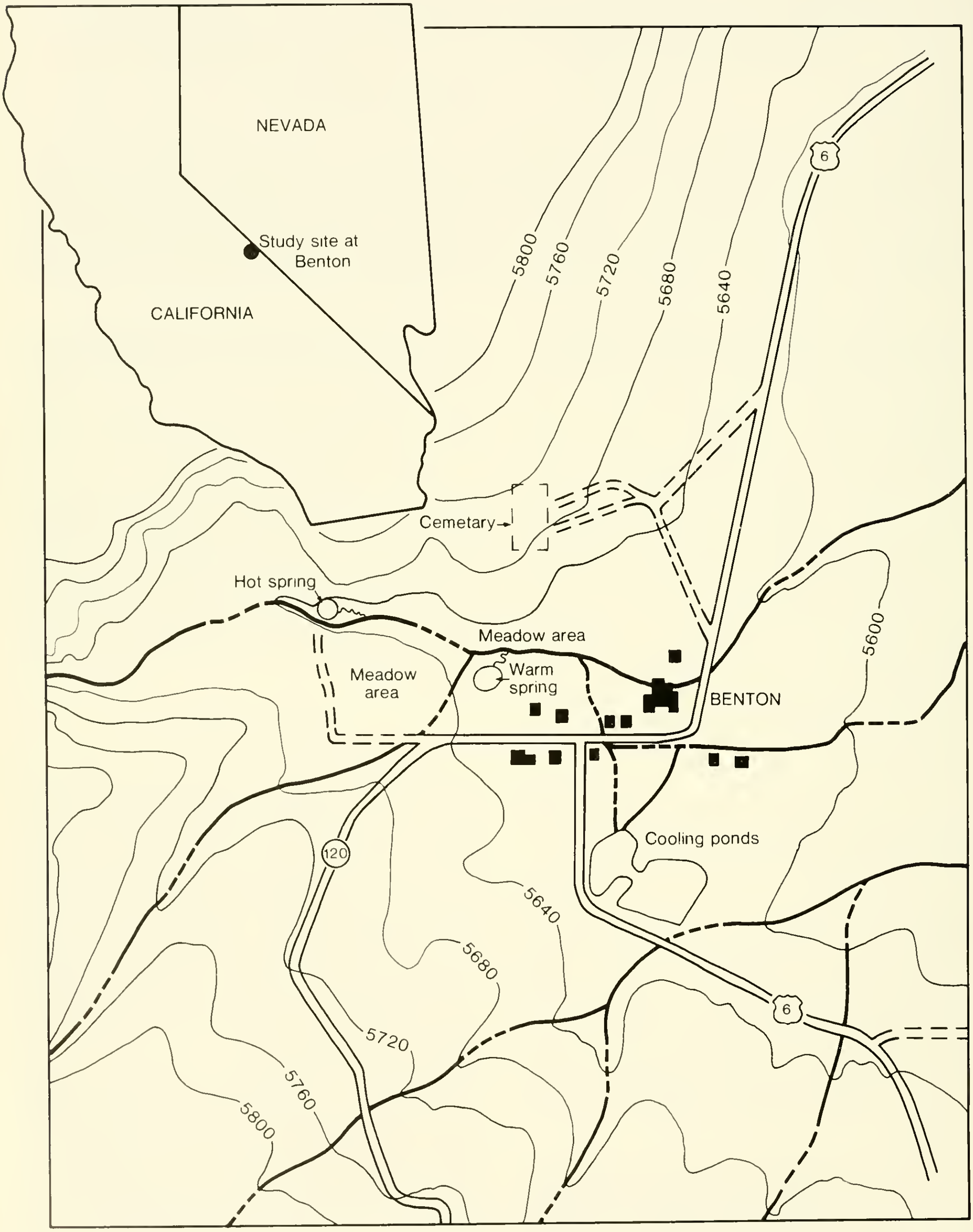
NEVADA
Study site at Benton
CALIFORNIA
5800
5760
5720
5680
5640
6
Cemetary
Hot spring
Meadow area
Meadow area
Warm spring
BENTON
5600
120
Cooling ponds
5640
5680
5720
5760
5800
6

Fig. 1. Map of study site at Benton, Mono County, California.

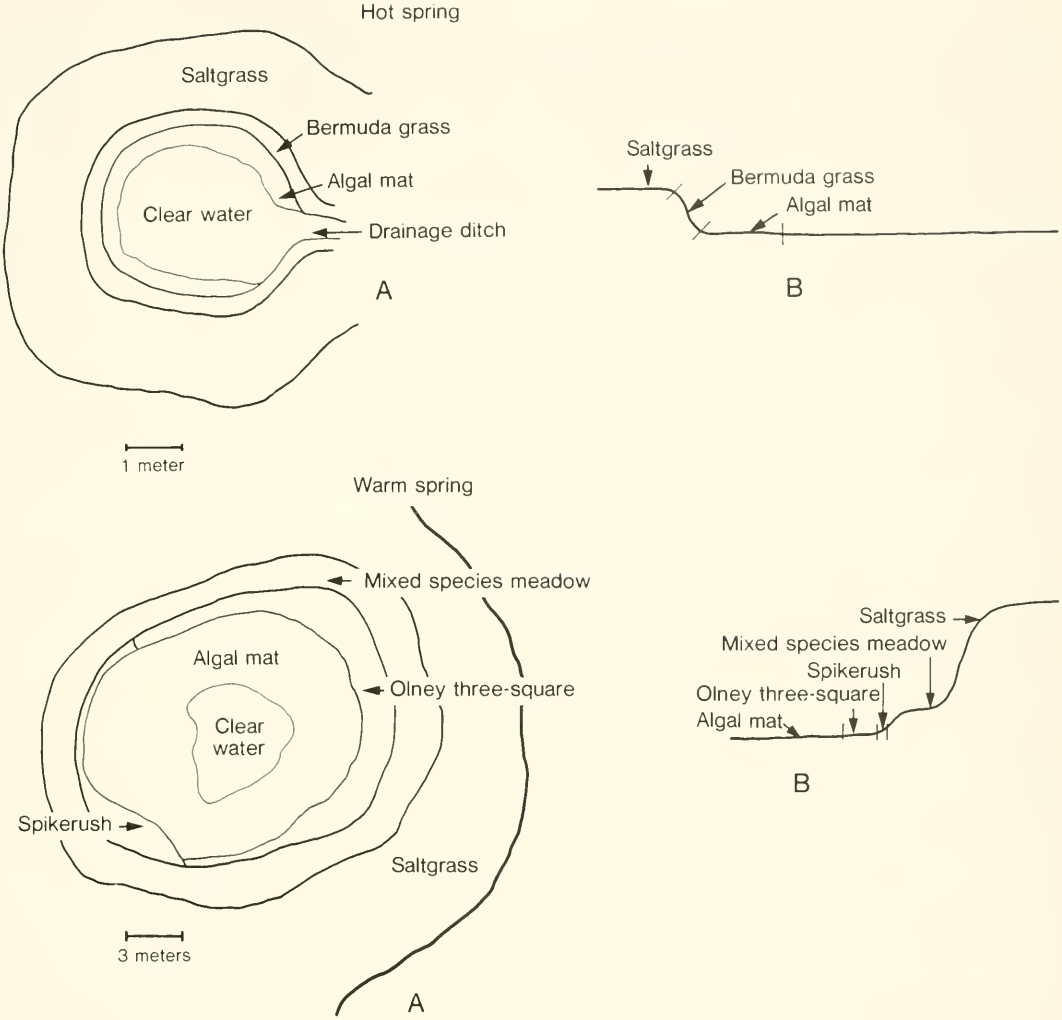
Hot spring
Saltgrass
Bermuda grass
Algal mat
Clear water
Drainage ditch
A
1 meter
Saltgrass
Bermuda grass
Algal mat
B
Warm spring
Mixed species meadow
Algal mat
Clear water
Olney three-square
Spikerush
Saltgrass
3 meters
A
Saltgrass
Mixed species meadow
Spikerush
Olney three-square
Algal mat
B

Fig. 2. Diagram of the vegetation patterns surrounding the hot and warm springs of the Benton Hot Springs complex. The As represent an overview and the Bs a profile view. The zones, listed by common name, relate to scientific names as follows: saltgrass (*Distichlis spicata*), bermuda grass (*Cynodon dactylon*), oleny three-square (*Scirpus americanus*), spikerush (*Eleocharis palustris*), and mixed-species meadow.

the aquatic areas showed well-developed algal mats.

Methods

Meadow vegetation was sampled using ten 15-m transects placed within each major zone surrounding the springs, stream, and cooling pond. Ten 0.25-m^2 quadrats were placed every 3 m along the transect. Data taken at each quadrat included total cover, cover by life form (Ostler 1980), and cover by species (Daubenmire 1959). Vegetation around each spring was visually mapped by zone.

Soil surface temperatures were determined according to zone by taking several temperatures and averaging the readings. A moisture index for the soils of each zone was assigned using the following scale: 1 = dry, 2 = moist, 3 = wet, 4 = seasonally inundated, and 5 = submerged (Brotherson and Evenson 1982). Two composite soil samples per zone were obtained for laboratory analyses by pooling a total of three samples from the top 20 cm of soil of each zone. These samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, and mineral content. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 g/v soil-water paste (Russell 1948) was used to determine pH and total soluble salts. Soils were extracted with a neutral 1.0 normal ammonium acetate solution for the analysis of calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils by use of DTPA (diethylenetriamine-pentaacetic acid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted by sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was made using macro-Kjeldahl procedures (Jackson 1958).

TABLE 1. Soil factors of the major vegetation zones found surrounding Benton Hot Springs. Zonation begins with the open water (I)* of the spring and progresses outward to the saltgrass meadow (V) next to the desert.

	Vegetation zone			
Soil factor	II	III	IV	V
Sand (%)	16.0	6.0	6.0	8.0
Silt (%)	32.0	16.0	9.0	22.0
Clay (%)	53.0	78.5	85.0	70.0
Fines (%)	84.0	94.0	94.0	92.0
pH	9.4	7.5	3.9	6.5
Soluble salts (ppm)	3010.0	802.0	1500.0	810.0
Nitrogen (%)	0.1	0.1	0.1	0.1
Phosphorus (ppm)	7.5	6.4	3.3	8.4
Calcium (ppm)	57.5	35.3	10.0	63.8
Magnesium (ppm)	1.0	1.5	1.0	3.3
Sodium (ppm)	2952.0	556.0	352.0	652.0
Potassium (ppm)	525.0	378.0	155.0	1025.3
Iron (ppm)	123.0	148.7	192.7	4.6
Zinc (ppm)	0.9	0.7	0.8	0.7
Manganese (ppm)	5.7	1.4	19.0	2.7
Copper (ppm)	0.4	0.6	0.5	0.5

*Data for Zone I are absent because of inaccessibility and high temperatures of spring water.

Plant nomenclature follows Munz (1968) for the dicotyledons and Cronquist et al. (1977) for the monocotyledons. Prevalent species were determined for the meadow following Warner and Harper (1972). Species diversity (MacArthur and Wilson 1967) was determined for each zone. Niche breadth was computed for each species and niche overlap was determined for all possible species pairs (Colwell and Futuyma 1971). Species were clustered according to the similarity of their occurrence in various zones of the study area. Cluster analysis was applied to niche overlap values (Sneath and Sokal 1973).

Data analysis consisted of computing means, standard deviations, and coefficients of variation for measured biotic and abiotic variables (Ott 1977). Interspecific association patterns between plant species were computed using Cole's Index (1949).

RESULTS AND DISCUSSION

Zonation patterns surrounding the Benton Springs are shown in Figure 2. In general, the zones formed concentric bands surrounding the open waters of the springs and parallel bands along the stream. These zones were related to the amount of water present in the soils. The hot spring showed two major terrestrial zones plus an algal mat at the edge of the open water. The warm spring had a more complex pattern of vegetation with four zones and an innermost algal mat. The zones surrounding the cooling pond and stream were similar to those about the warm spring except that lily pads formed a fifth distinct zone in the cooling pond where algal mats were absent.

Results of our soil analyses are presented in Table 1. Several of the soil variables showed differences between vegetation zones. For example, percent sand and silt, soluble salts, and sodium were high in Zone 2 and decreased outward. Also, the patterns relating to Zone 4 are of interest when compared to those of Zones 3 and 5 (Table 1). For example, pH dropped from circumneutral in Zones 3 and 5 to highly acidic in Zone 4. In addition, soluble salts and manganese were elevated in Zone 4, while calcium, sodium, and potassium decreased in this zone. Iron showed a 20-fold decrease from Zones 2 through 4 to Zone 5. Manganese and potassium also increased in Zone 5. Nitrogen, zinc, and copper showed no changes through any of the vegetation zones. No soil samples were collected from Zone 1 because of inaccessibility and high temperatures of the spring water.

Soil moisture and surface temperature showed an inverse relationship when moving from Zone 1 through Zone 5, with soil moisture decreasing as soil surface temperature increased (Table 2). Where soil moisture levels are highest, greater evaporation occurs

TABLE 2. Site factors of the major vegetation zones found surrounding Benton Hot Springs. Zonation begins with the open water of the spring (I) and progresses outward to the saltgrass meadow (V) next to the desert.

	Vegetation zone				
Site factor	I	II	III	IV	V
Total cover	100.0	100.0	100.0	100.0	86.0
Soil temperature (surface)	28.7	24.7	39.0	34.4	45.6
*Moisture	5.0	4.0	3.3	2.5	2.0
No. of sp/quad	1.0	4.2	4.1	3.4	3.2
% sedge cover	100.0	85.0	13.7	27.9	4.4
% grass cover	0.0	13.8	85.6	64.5	81.5
% forb cover	0.0	0.0	0.1	0.0	0.0
% shrub cover	0.0	1.2	0.4	7.6	9.6
% annual cover	0.0	0.0	0.2	0.0	4.4
Total # of species/zone	1.0	9.0	11.0	7.0	16.0
% composition by cover of rhizome species	100.0	97.6	93.0	94.0	86.5
No. of species contributing 90% of cover	1.0	3.0	7. 0	6.0	8.0
Diversity ($1/\Sigma pi^2$)	1.0	1.7	3.06	2.36	1.54

*Moisture index is as follows: 1 = dry; 2 = moist; 3 = wet; 4 = seasonally inundated, and 5 = submerged (Brotherson and Evenson 1982).

and therefore cooling is increased at the soil surface. Also, vegetation cover was generally greater in the zones with increased moisture.

Species diversity (MacArthur and Wilson 1963), which peaked in the middle zones, was lowest in the inner (wettest) zone surrounding the springs and was also depressed in the outermost (driest) zone (Table 2). In contrast, the total number of species as well as the number of species contributing greater than 90% of the cover increased from Zone 1 through Zone 5.

Life-form data (Table 2) showed sedge cover to be totally dominant in Zone 1, decreasing to near 0 in Zone 5. Grass and shrub cover were absent in Zone 1 and generally increased moving away from the springs. Forb and annual cover were generally insignificant in the Benton flora. Those species showing asexual reproduction by rhizomes generally decreased from Zone 1 to Zone 5, which corresponds to similar decreases in moisture and sedge cover. Schaffer and Gadgil (1975) suggest that this pattern of increased asexual reproduction is to be expected where stable environments exist. Where moisture levels are high, for instance in the areas near the springs, the environments should be more constant.

A total of 25 vascular plant species were encountered in the Benton Hot Springs flora. All species showed restriction to one or more of the vegetation zones (Table 3). Many of the species were restricted to a single zone, while *Juncus balticus* was present in four of the zones.

Species cover values were subjected to niche breadth and overlap analyses (Colwell and Fatuyma 1971). These analyses showed eight cluster groups, two of which represented single species (Fig. 3). In most cases the groups were loosely defined, although between-group similarity was very low when compared to within-group similarity. Generally, the groups appear to represent actual species distribution patterns within the vegetation zones surrounding the springs. For example, Group D represents species restricted to or dominant in Zone 2 (Table 3), which is the zone immediately adjacent to the thermal water. Similarly, Group B represents two species that occurred primarily in the wet areas of Zone 3, and Group G is comprised of taxa found in the outermost zone near the desert. Group A represents an assemblage of species dominant in the outer three zones.

In an attempt to assess which of the species groups, delineated by clustering on niche overlap, represented significant positive associations, we employed Cole's Index of interspecific association (Cole 1949). This analysis yielded a number of significant positive associations (Table 4). In most cases, the patterns of association delineated by the cluster analysis (Fig. 4) were shown by interspecific-association analysis to be significant. Such positive associations would indicate that the species involved are generally adapted to similar habitat conditions and therefore will often be found together where such conditions exist.

Prevalent species in the Benton Hot Springs flora are listed in Table 5. The most

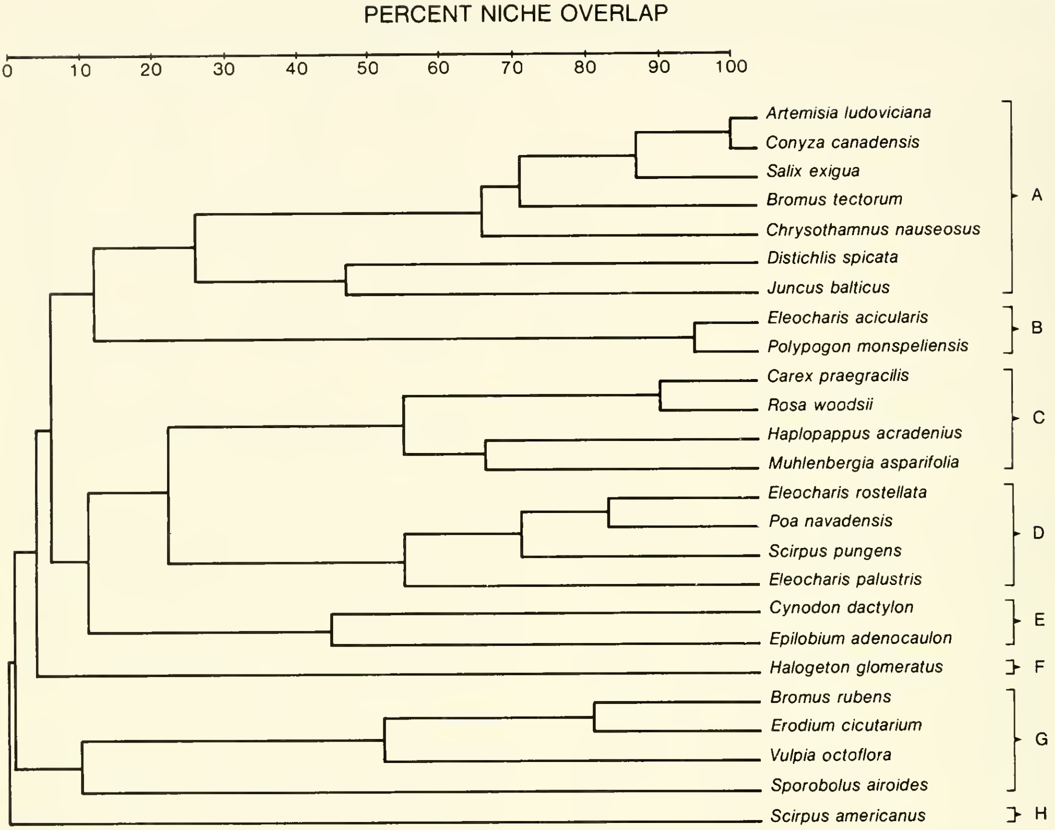
PERCENT NICHE OVERLAP
0
10
20
30
40
50
60
70
80
90
100
Artemisia ludoviciana
Conyza canadensis
Salix exigua
Bromus tectorum
Chrysothamnus nauseosus
Distichlis spicata
Juncus balticus
Eleocharis acicularis
Polypogon monspeliensis
Carex praegracilis
Rosa woodsii
Haplopappus acradenius
Muhlenbergia asparifolia
Eleocharis rostellata
Poa navadensis
Scirpus pungens
Eleocharis palustris
Cynodon dactylon
Epilobium adenocaulon
Halogeton glomeratus
Bromus rubens
Erodium cicutarium
Vulpia octoflora
Sporobolus airoides
Scirpus americanus
A
B
C
D
E
F
G
H

Fig. 3. Cluster dendrogram of plant species occurring in the study area grouped on the basis of niche overlap. Niche overlap values were based on frequency data relative to a species geographical distribution.

important species was *Distichilis spicata*, followed by *Muhlenbergia asperifolia*, *Cynodon dactylon*, and *Juncus balticus*. The distribution patterns of *Distichilis spicata* and *Cynodon dactylon* are of interest. Away from the influence of the thermal water, these species often grew intermingled. However, near the water, *C. dactylon* formed a monospecific zone that was replaced by *D. spicata* just centimeters away from the hot water. The natural distribution of *D. spicata* ranges into areas of the western U.S. where climatic conditions tend to be cold over much of the year. In contrast, the natural distribution of *C. dactylon* ranges across much of the southern U.S. where the climate is mostly hot and humid and where frosts are rare. Since *C. dactylon* is adapted to such environments, its response to the elevated heat levels of the spring water and its competitive edge under such conditions near the spring are understandable.

Starting at the open water of the spring and moving toward the desert, a distance of some 100 m, a distinct moisture gradient is apparent. The major species in the vegetation sort well along this gradient. The dominant species of this zonation pattern are shown in Figure 4. In the open-water areas, lily pads and algal mats dominate. The zones at the water's edge are generally single-species dominated and include *Scirpus americanus* and *Eleocharis palustris*. Through the middle portion of this moisture gradient, several species are important. In the outer and drier part of the gradient, the zones are again dominated by one or two taxa, with *D. spicata* increasing in importance away from the springs.

TABLE 3. Average percent cover values of plant species associated with major vegetation zones surrounding Benton Hot Springs. Zonation starts at the open water of the spring (I) and progresses outward to the saltgrass meadow (V) next to the desert.

	Vegetation zone				
Species	I	II	III	IV	V
Scirpus americanus	97.5	3.5			
Eleocharis palustris		88.0	14.8		
Muhlenbergia asperifolia		17.0	28.3		0.6
Juncus balticus		12.5	0.5	30.0	4.4
Scirpus pungens		3.0		1.1	
Eleocharis rostellata		3.0			
Haplopappus acradenius		2.0	0.3	1.6	
Polypogon monspeliensis		0.5	7.8		
Poa navadensis		0.5			0.1
Cynodon dactylon			55.2		6.1
Distichlis spicata			15.7	61.0	73.4
Eleocharis acicularis			1.8		
Epilobium adenocaulon			0.2		
Chrysothamnus nauseosus			0.3	4.2	6.8
Bromus tectorum			0.3		0.1
Carex praegracilis				6.9	
Rosa woodsii				1.5	
Halogeton glomeratus					0.2
Bromus rubens					1.1
Sporobolus airoides					0.1
Erodium cicutarium					1.5
Vulpia octiflora					0.9
Conyza canadensis					0.1
Artemisia ludoviciana					0.1
Salix exigua					0.1

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TABLE 4. Cole's Index values expressing positive and/or negative interspecific association between species found adjacent to Benton Hot Springs.

Species	Species	X^{2a}	C_7^{b}	SD_7^{c}
Artemisia ludoviciana	*Bromus tectorum*	24.99	1.00	0.20
	Conyza canadensis	51.00	1.00	0.14
	Salix exigua	24.99	1.00	0.20
Bromus rubens	*Erodium cicutarium*	24.46	0.48	0.09
	Muhlenbergia asperifolia	3.86	−1.00	0.51
	Sporobolus aeroides	11.98	0.24	0.07
	Vulpia octoflora	24.46	0.48	0.09
Bromus tectorum	*Conyza canadensis*	25.00	0.49	0.09
	Eleocharis acicularis	11.73	0.48	0.14
	Salix exigua	11.73	0.48	0.14
Carex praegracilis	*Halogeaton glomeratus*	9.83	0.70	0.22
	Juncus balticus	7.96	1.00	0.35
	Rosa woodsii	11.99	0.24	0.07
Chrysothamnus nauseosus	*Eleocharis palustris*	3.83	−1.00	0.51
	Salix exigua	6.76	0.13	0.05
Conyza canadensis	*Salix exigua*	25.00	1.00	0.20
Cynodon dactylon	*Eleocharis acicularis*	4.55	0.09	0.04
	Muhlenbergia asperifolia	10.94	0.65	0.19
	Poa navadensis	11.13	0.28	0.08
Distichlis spicata	*Eleocharis palustris*	6.62	−0.45	0.17
	Halogeton glomeratus	4.33	−0.39	0.19
	Juncus balticus	6.69	0.16	0.06
	Scirpus americanus	14.65	−1.00	0.26
	Scirpus pungens	4.93	−0.66	0.30
Eleocharis palustris	*Eleocharis rostellata*	4.18	0.08	0.04
	Epilobium adenocaulon	4.18	0.08	0.04
	Halogeton glomeratus	4.28	0.27	0.13
	Muhlenbergia asperifolia	13.99	1.00	0.27
	Scirpus pungens	8.45	0.24	0.08
Eleocharis rostellata	*Halogeton glomeratus*	4.76	1.00	0.46
	Poa navadensis	6.41	1.00	0.39
	Polypogon monspeliensis	24.99	1.00	0.20
	Scirpus pungens	11.99	1.00	0.29
Erodium cicutarium	*Vulpia octoflora*	11.73	0.48	0.14
Halogeton glomeratus	*Muhlenbergia asperifolia*	4.14	0.58	0.29
	Rosa woodsii	4.76	0.09	0.04
	Muhlenbergia asperifolia	9.13	0.18	0.06
	Scirpus americanus	4.93	−1.00	0.45
Polypogon monspeliensis	*Scirpus pungens*	5.12	0.46	0.20

a = Chi-square; b = Cole's Index; c = standard deviation of Cole's Index.

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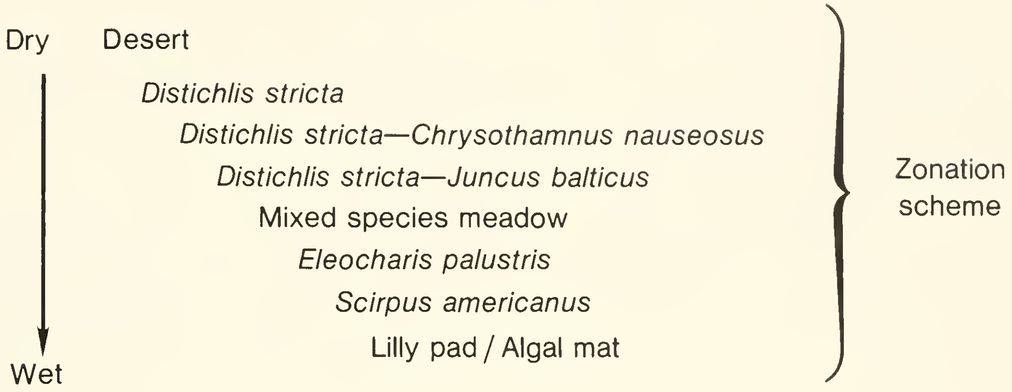
Dry
Desert
Distichlis stricta
Distichlis stricta—Chrysothamnus nauseosus
Distichlis stricta—Juncus balticus
Mixed species meadow
Eleocharis palustris
Scirpus americanus
Lilly pad / Algal mat
Wet
Zonation scheme

Fig. 4. Schematic diagram of vegetation patterns in the meadows surrounding the hot and warm springs complex at Benton, Mono County, California. Listed are the major dominants of each zone in relation to their placement along a moisture gradient beginning at the spring and ending in the desert.

Table 5. Prevalent species associated with the vegetation surrounding Benton Hot Springs along with their importance values; the P × C index is based on percent presence of a species in the different zones multiplied by its mean cover across all zones.

Species	P × C Index
Distichlis spicata	38.0
Muhlenbergia asperifolia	8.8
Cynodon dactylon	5.9
Juncus balticus	4.4
Eleocharis palustris	3.2
Scirpus americanus	1.2
Chrysothamnus nauseosus	0.7

NEW BRACHIOSAUR MATERIAL FROM THE LATE JURASSIC OF UTAH AND COLORADO

James A. Jensen[1]

ABSTRACT.—Little is known about the Brachiosauridae, which includes some of the largest known sauropods, such as the genus *Brachiosaurus*, discovered in western Colorado by Elmer S. Riggs in 1900. Additional diagnostic material, previously unknown in the western hemisphere, is reported from three comparatively recent quarries: the Jensen/Jensen Quarry in eastern Utah and the Dry Mesa and Potter Creek quarries on the Uncompahgre Upwarp in western Colorado. An unknown, well-preserved, articulated sauropod atlas/axis, seven cervical vertebrae, and an interesting flora were associated with the Potter Creek Quarry brachiosaur material. Taphonomic factors in that quarry are noted. The Jensen/Jensen and Dry Mesa deposits occur in basal sediments of the Brushy Basin Member of the Morrison Formation, and the Potter Creek Quarry in an intermediate section of that member.

No complete, articulated skeleton of the sauropod genus *Brachiosaurus* has been reported from North America. However, an incomplete skeleton was collected in Colorado in 1901, and disarticulated bones of the genus have been found in at least four other localities. Elements described here, not previously reported from the western hemisphere, include a partial scapula, a distal cervical vertebra, a radius, a metacarpal, and a humerus. The radius, metacarpal, and humerus appear to represent a novel species but will not be described here as such.

In 1900 the type-species of the genus *Brachiosaurus* was collected by Elmer S. Riggs, of the Field Columbian Museum, Chicago, who discovered a partial skeleton of this remarkable sauropod near Grand Junction, Colorado. This skeleton possessed the previously unknown feature of front legs equal in length to the rear (Fig. 1), which elevated the base of the neck and thorax far above any spinal inclination previously reported in sauropods. Riggs (1903) appropriately named it *Brachiosaurus altithorax*. He recovered approximately 20 bones, including seven articulated presacral and two caudal vertebrae, a sacrum and the right ilium, a left coracoid, right humerus, right femur (Fig. 1), and four ribs. The femur and humerus were greatly compressed, with the distal end of the latter being partially destroyed by surface erosion (Fig. 1). This material is now preserved in the Field Museum of Natural History, Chicago.

A decade later a second discovery of brachiosaur bones was collected by a German paleontologist, Janensch, in Tendaguru, Tanzania, formerly East Africa. He recovered a fairly complete skeleton that he named *B. brancai* (Janensch 1914); the restored skeleton is now mounted in the Museum für Naturkunde in East Berlin, East Germany. Subsequent work by British expeditions, and possibly other European institutions, recovered other brachiosaur materials from Tanzania, but for more than 80 years no additional brachiosaur remains were scientifically reported from the western hemisphere.

Circa 1943 a brachiosaur skeleton in an advanced state of erosion was discovered on the Uncompahgre Upwarp in western Colorado by the late Daniel E. Jones and his wife, Vivian, of Delta, Colorado. The humerus (Figs. 2B, 3A–D, 4B) was collected and donated to the U.S. National Museum in Washington, D.C., but was never described. The discovery site, approximately 70 km SSE of the Riggs locality, was named the Potter Creek Quarry. Its stratigraphic position is approximately in the middle of the Brushy Basin Member of the Morrison Formation. I worked there two seasons (1971, 1975), collecting five disarticulated elements of a large sauropod (? *B. altithorax*), bones of a second, smaller sauropod genus, and teeth of an unknown theropod. The brachiosaur elements collected include part of the discovery humerus (Figs. 3E, 5A–D, 6B), a medial

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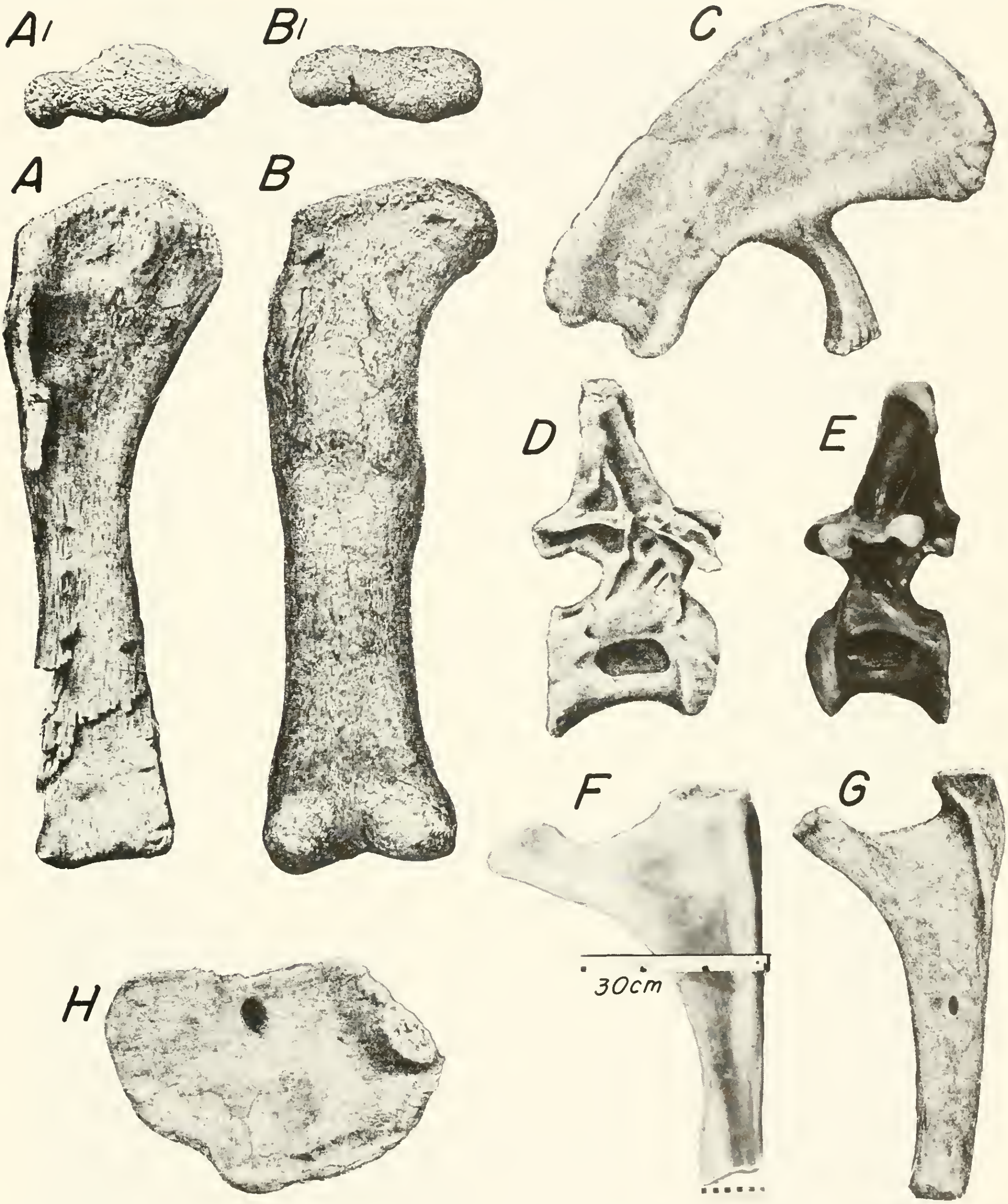

Fig. 1. A–D, F–H, elements of the type of *Brachiosaurus altithorax* (from Riggs 1904): A, humerus, anterior view; A_1, proximal end; B, femur, anterior view; B_1, proximal end view; C, right ilium; D, fifth presacral vertebra; E, Potter Creek Quarry brachiosaur, fourth or fifth presacral vertebra; F, thoracic rib head, anterior view; G, *B. altithorax*, thoracic rib head, mesio-anterior view; H, *B. altithorax*, lateral view of left coracoid. Scale: A–D, F–H, approximately 1/12 natural size.

dorsal vertebra (Figs. 3D, 4A–A_3), an incomplete left ilium (Fig. 3A–A_2), and a left radius and metacarpal (Figs. 3B, 5E–E_1). Materials of the smaller, indeterminate sauropod include the broken fragments of an articulated vertebral series from the atlas/axis to the seventh cervical vertebra. This series was found intact but excavated in fragments by the Jones family and given to me. I was able to reassemble an articulated atlas/axis and third cervical

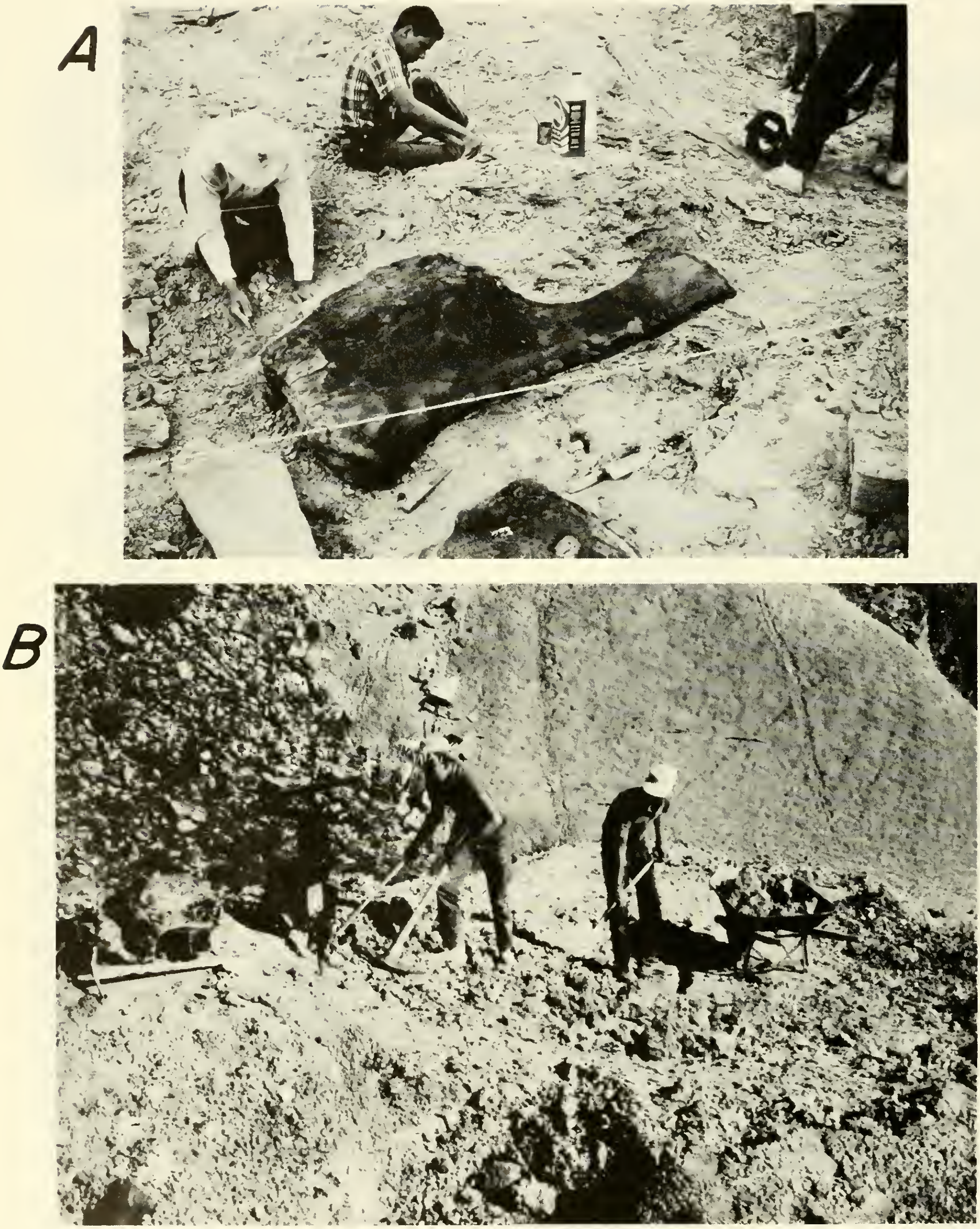

Fig. 2. A, Jensen/Jensen Quarry: scapula with coracoid in foreground (the only existing illustration of these unprepared brachiosaur elements); worker in upper right corner is sawing around border of 9′ brachiosaur rib; B, Potter Creek Quarry.

vertebra (Fig. 10A–E) from this broken material because of its excellent preservation. A detailed study of some of this material is in progress, but a preliminary examination reveals it to be from a mature sauropod. The elements noted here are much too short and small for any described brachiosaurid.

In 1960 I discovered a dinosaur bone deposit in basal Brushy Basin Member sediments of the Morrison Formation near

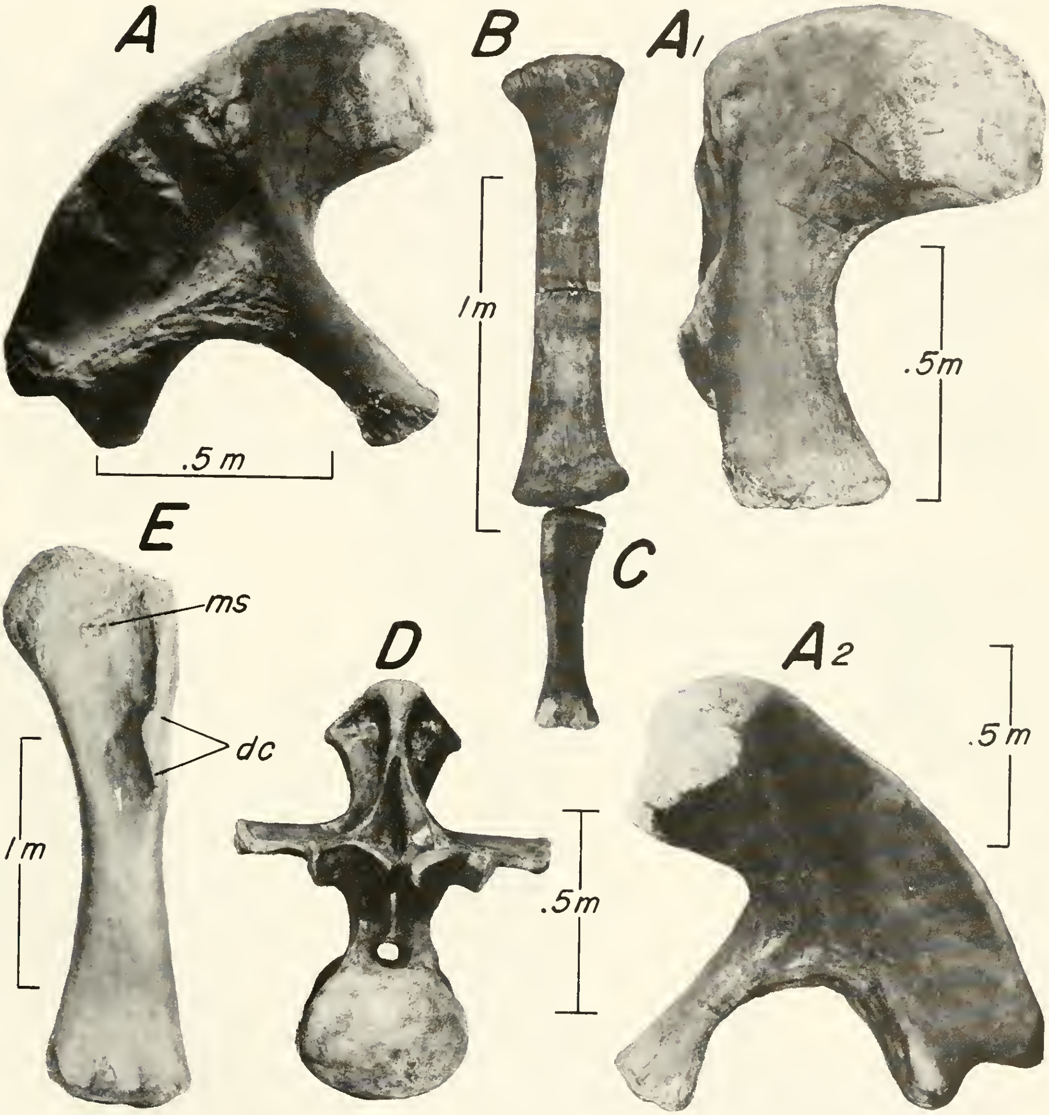

Fig. 3. Potter Creek Quarry brachiosaur: A–A_2, left ilium (dorsal border, ischiadic peduncle restored); B, radius; C, metacarpal; D, fourth or fifth dorsal vertebra; E, left humerus. Abbreviations: dc, deltoid crest; ms, muscle fossa.

Jensen, Utah. This deposit (the Jensen/Jensen Quarry) is located south of the Green River, a few miles from the Dinosaur National Monument Quarry. Two years' work (1962, 1966) in this quarry (Figs. 11, 13) produced several brachiosaur elements including a rib 2.75 m (9 ft) long (Fig. 6B), a distal cervical vertebra, the proximal half of a scapula, and a coracoid. Many worthless slivers and fragments of shattered brachiosaur cervical vertebrae were encountered. Because the coracoid associated with the scapula does not appear to match the coracoid of *B. altithorax*, the specific identity of the elements is presently in question. When fully prepared, the material may represent an undescribed species; but an insufficient number of elements duplicating those of the type-species presently precludes such a determination. Additional, well-preserved brachiosaur material, cited in the Uncompahgre fauna (Jensen 1985), is described here from the Potter Creek Quarry.

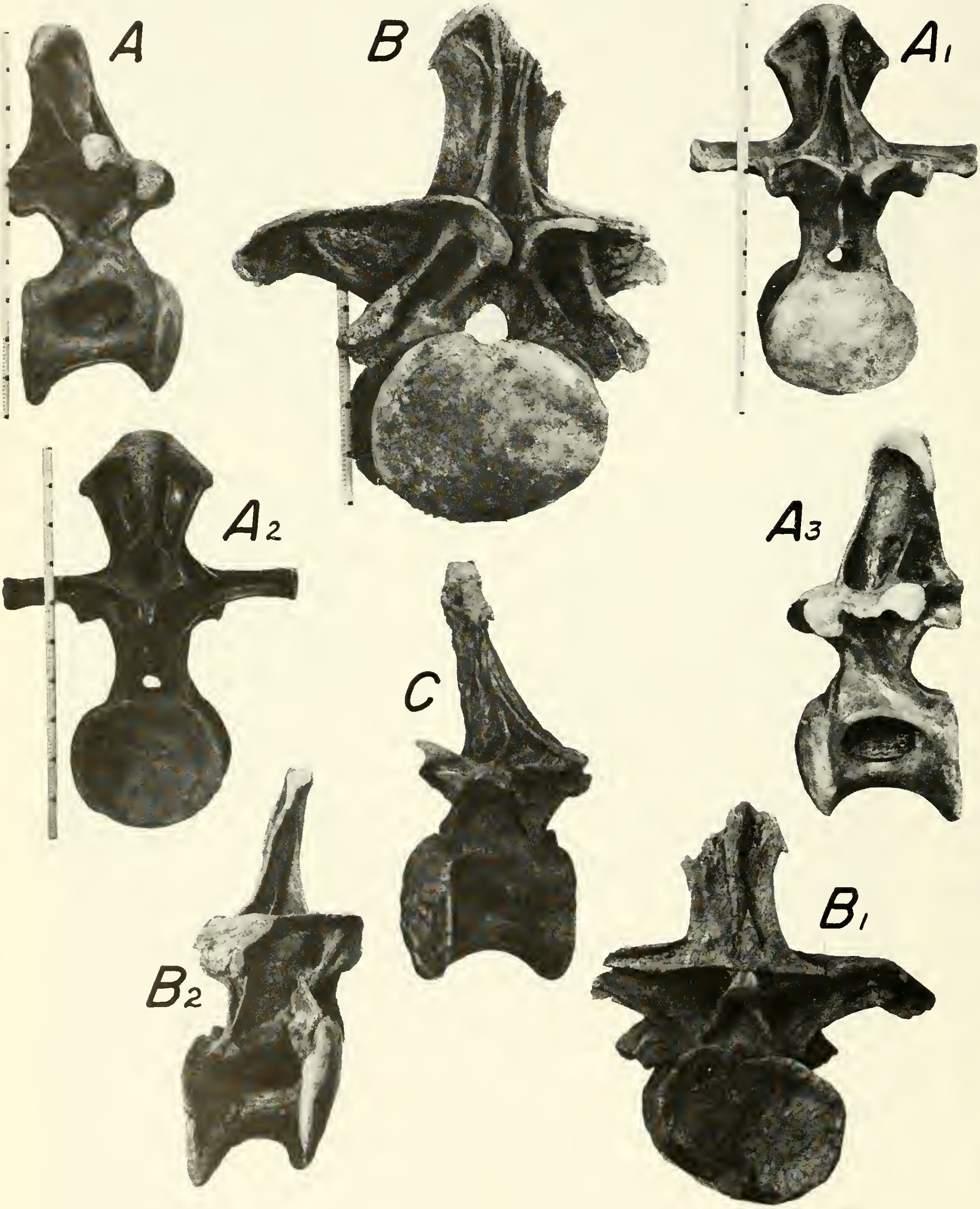

Fig. 4. Dorsal vertebrae: A–A$_3$, Potter Creek Quarry brachiosaur, fourth or fifth dorsal vertebra, right lateral view; B–B$_2$, *Dystylosaurus edwini*, type (B), anterior (B$_1$), posterior (B$_2$), right lateral views, probably anterior dorsal; C, *Ultrasaurus macintoshi*, type posterior dorsal vertebra, 1.45 m tall, left lateral view.

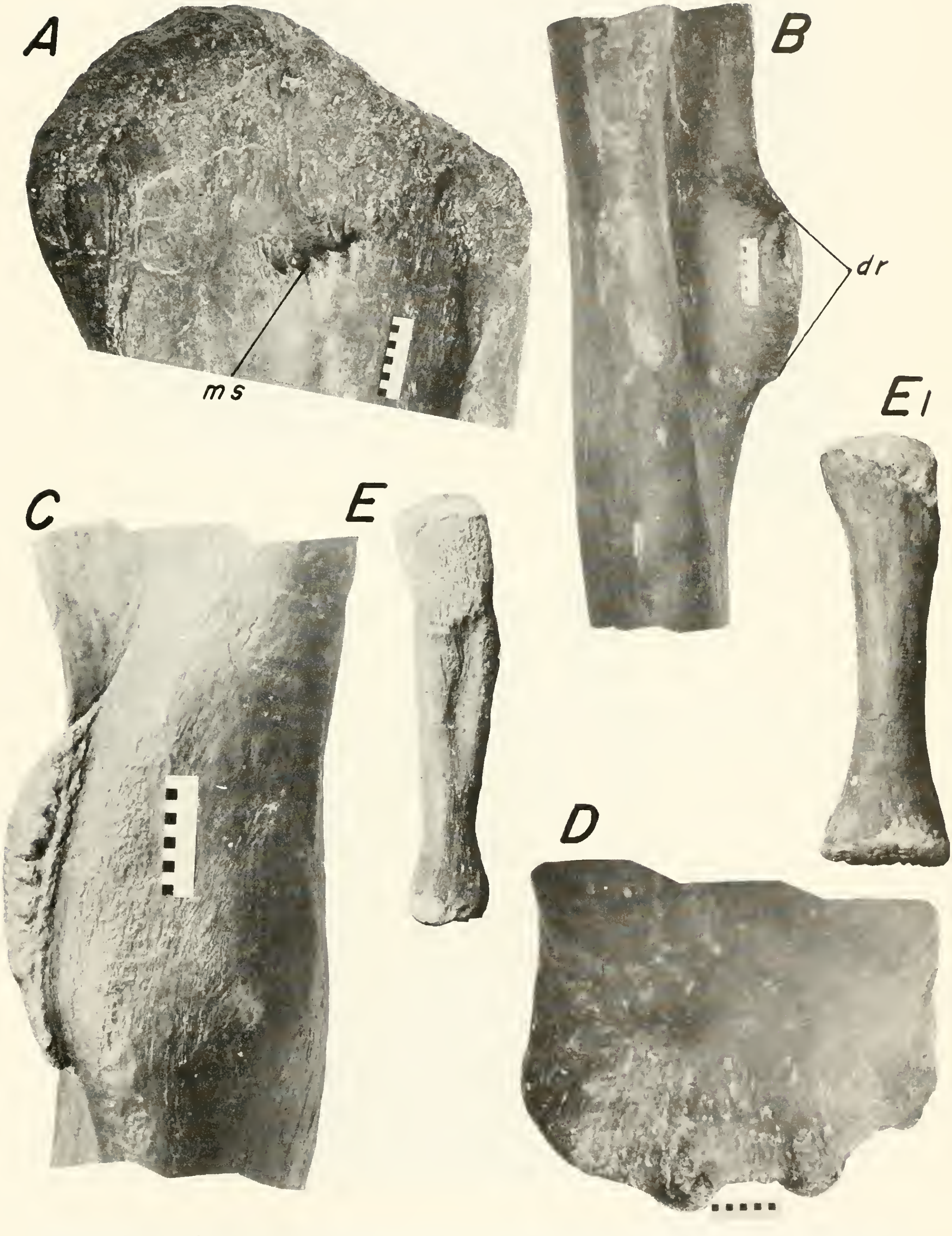

Fig. 5. Potter Creek Quarry: A–D, brachiosaur humerus. A, proximal end; B, mid-shaft section; C, detail of bulbous deltoid crest; D, anterior, distal end; E, metacarpal MC I, mesial view; E_1, same, lateral view. Abbreviations: dr, deltoid ridge; ms, muscle fossa/scar.

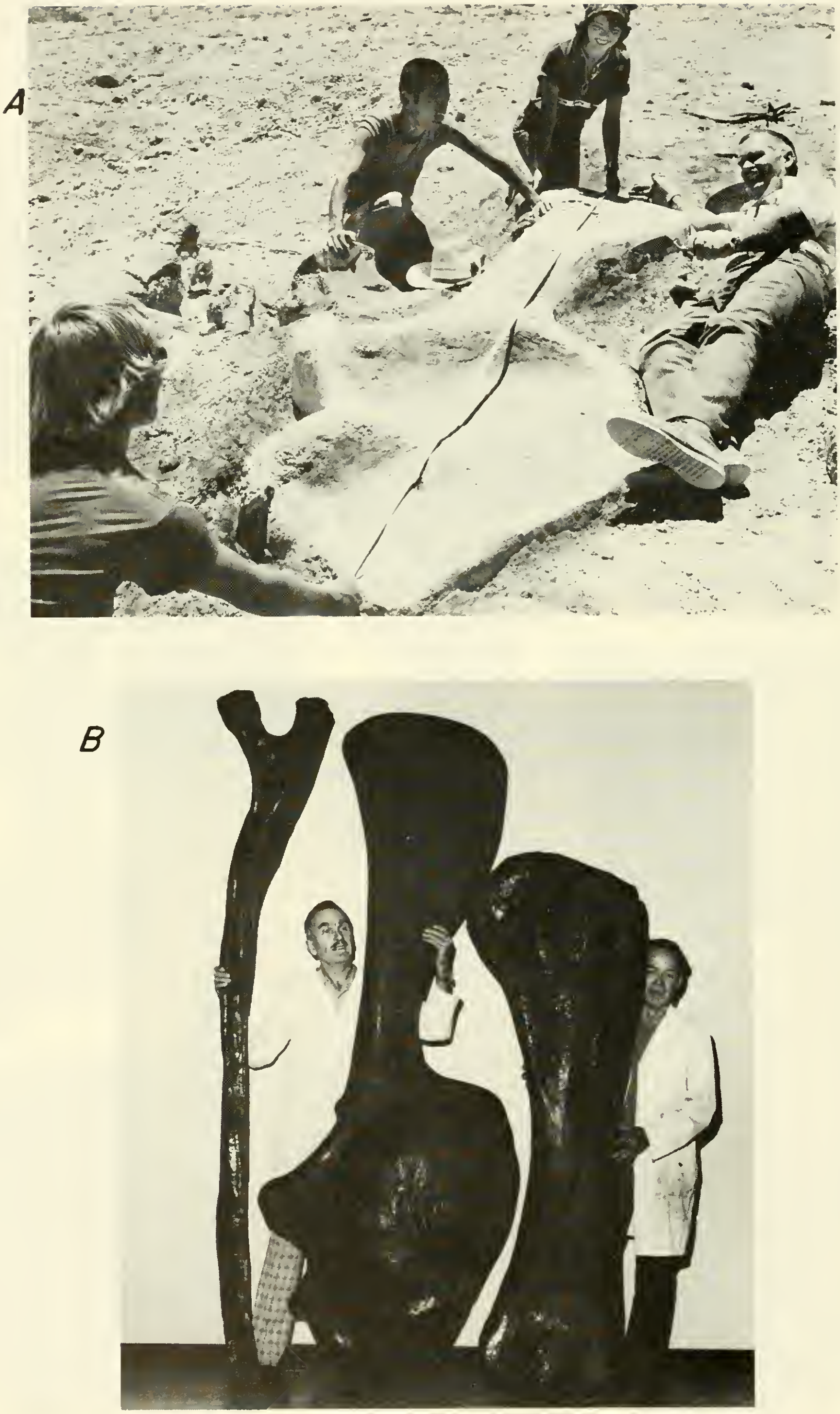

Fig. 6. A, Scapulocoracoid referred to *Ultrasaurus macintoshi*, prone figure 6′3″ tall; B, Jensen/Jensen Quarry brachiosaur rib, Dry Mesa Quarry *Ultrasaurus* scapulocoracoid, Potter Creek Quarry brachiosaur left humerus. All three elements cast in fiberglass resin.

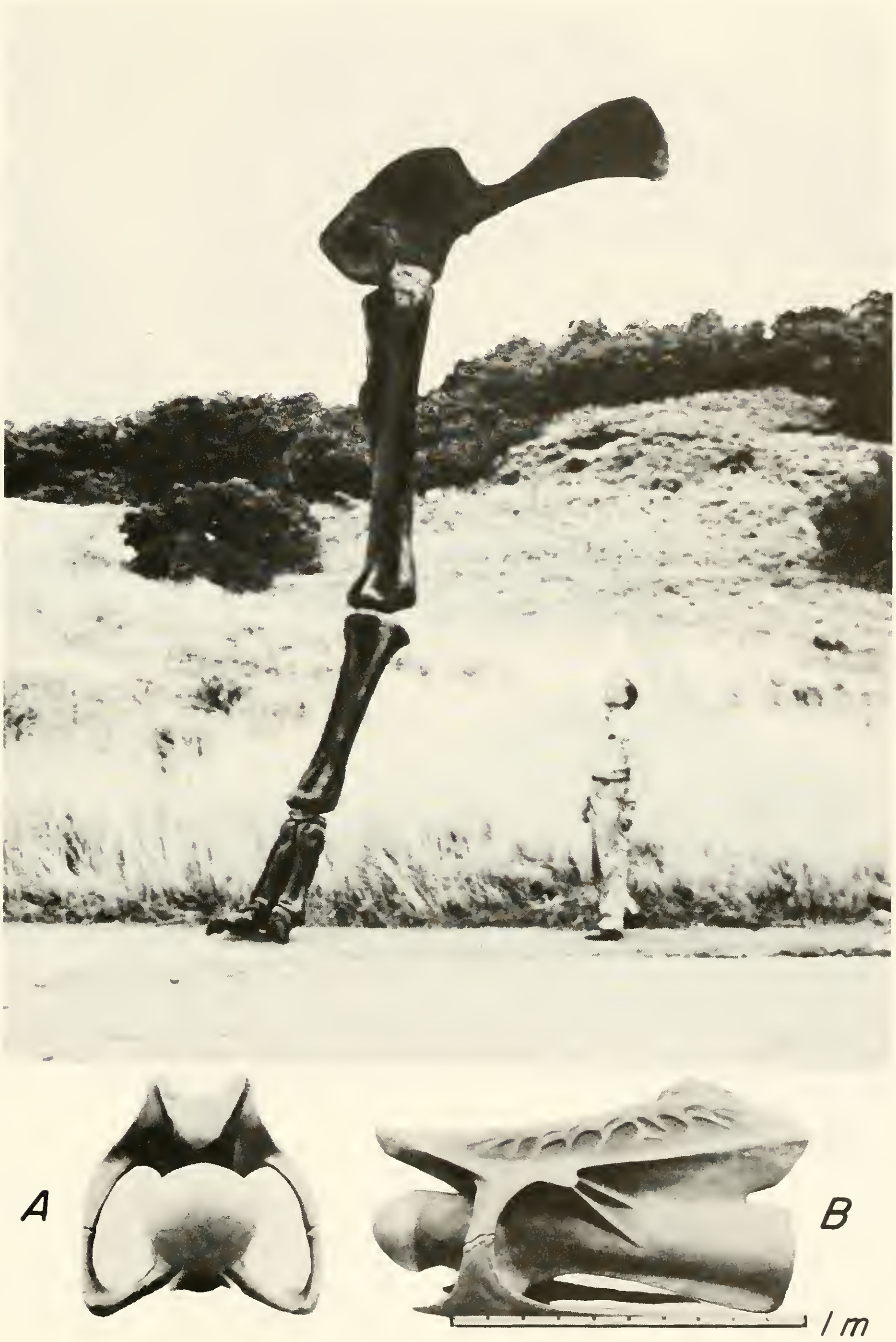

Fig. 7A–B. Reconstructed front limb with cast scapulocoracoid of *Ultrasaurus macintoshi* (figure 6′3″ tall): A, mid-cervical vertebra, *Supersaurus vivianae*, anterior view (original seen in Fig. 8); B, same, left lateral view. Vertebra restored from original and cast in fiberglass resin.

This material is much better preserved than that of the type of *B. altithorax* (Riggs 1903) and justifies some revision of the generic diagnosis (see SYSTEMATIC PALEONTOLOGY).

In 1972 I opened a quarry near Dry Mesa (Dry Mesa Quarry) in basal Brushy Basin

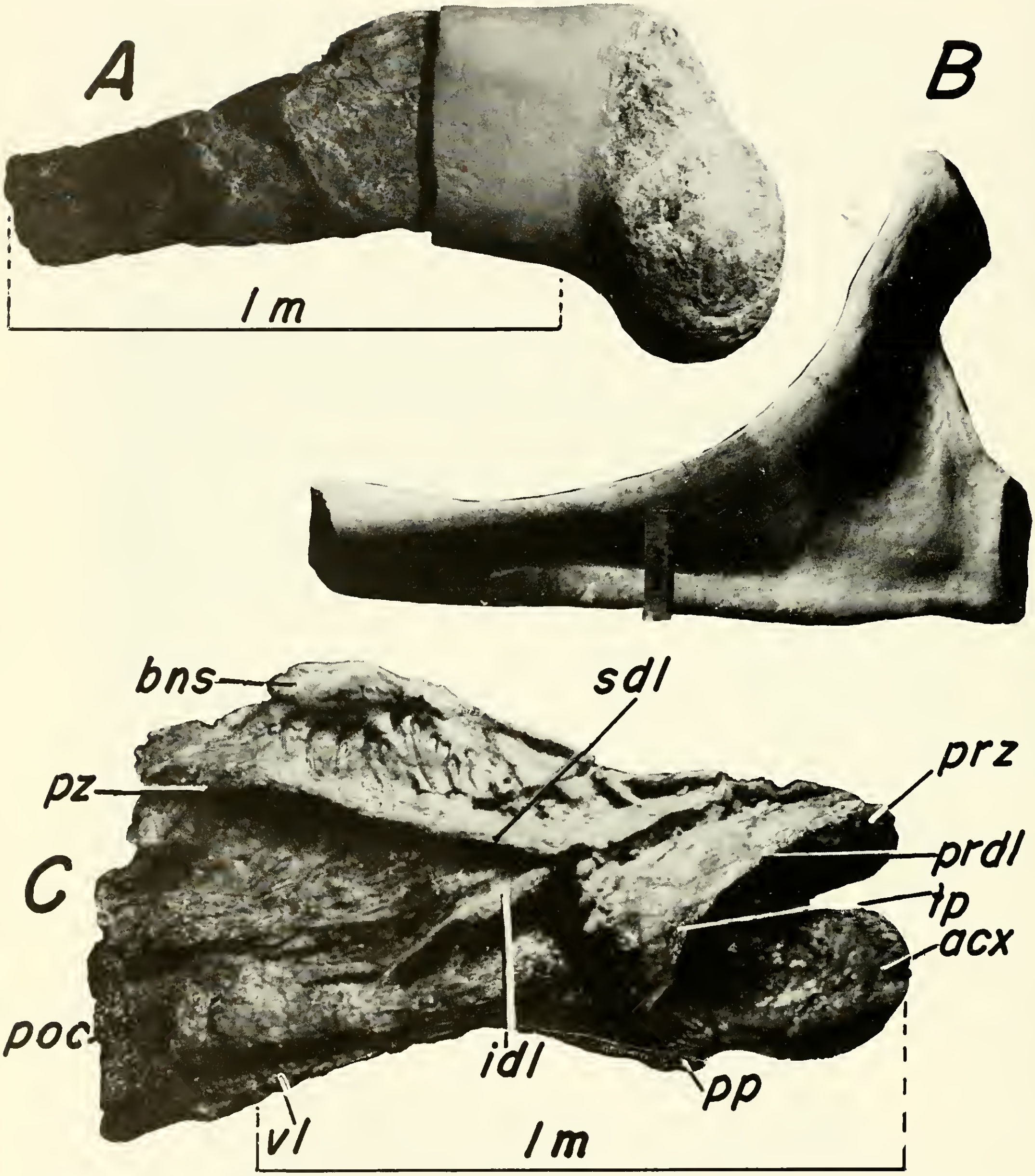

Fig. 8. A, Proximal end of brachiosaur femur, proximal end 5′6″ in circumference, from Recapture Member of the Morrison Formation; B, *Supersaurus vivianae*, right lateral view of mid-cervical vertebra; C, mid-cervical vertebra, *Supersaurus vivianae* right lateral view (restoration seen in Fig. 7). Abbreviations: acx, anterior convexity; bns, bifurcate neural spine; idl, infradiagonal lamina; poc, posterior concavity; pp, parapophysis; prdl, prediapophysial lamina; prz, prezygapophysis; pz, postzygapophysis; sdl, supradiagonal lamina; tp, transverse process; vl, ventral lamina.

Member sediments on the NE monocline of the Uncompahgre Upwarp in western Colorado. This quarry (Fig. 13) lies approximately 20 km NW of the Potter Creek Quarry but is on a significantly lower horizon. A decade of work in it produced many tons of dinosaur-related materials including bones of several unusually large sauropods (Jensen 1985), some of which appear to be brachiosaurid. Among the large elements recovered was a (?) mid-cervical vertebra more than 1 m in length (Figs. 7A–B, 8C), which, having a bifurcate

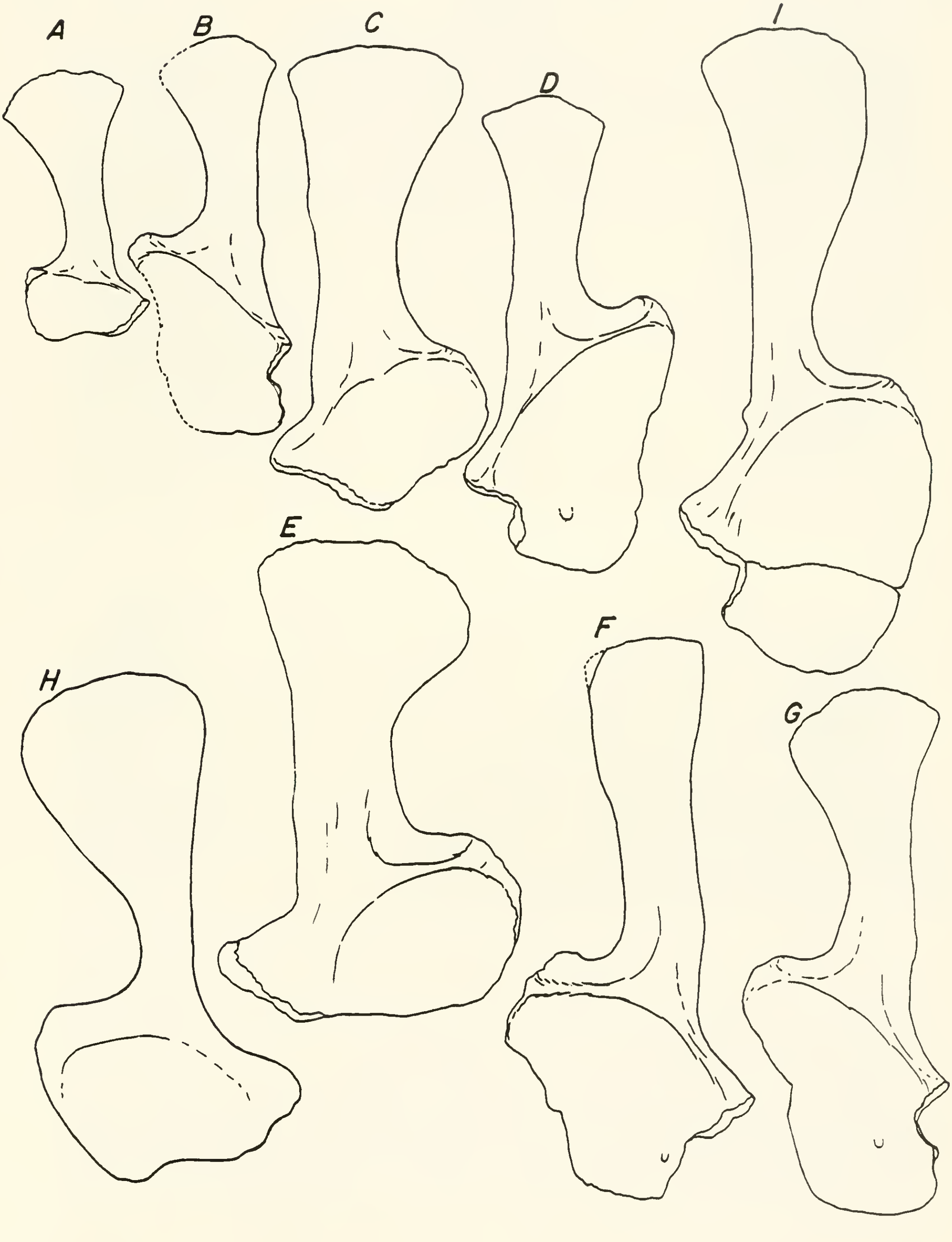

Fig. 9. Scapula (coracoid) profiles of eight sauropod genera: A, *Haplocanthosaurus;* B, *Supersaurus vivianae;* C, *Cetiosaurus;* D, *Diplodocus;* E. *Camarasaurus;* F, *Apatosaurus;* G, *Supersaurus;* H, *Brachiosaurus;* I, *Ultrasaurus.* Not to scale.

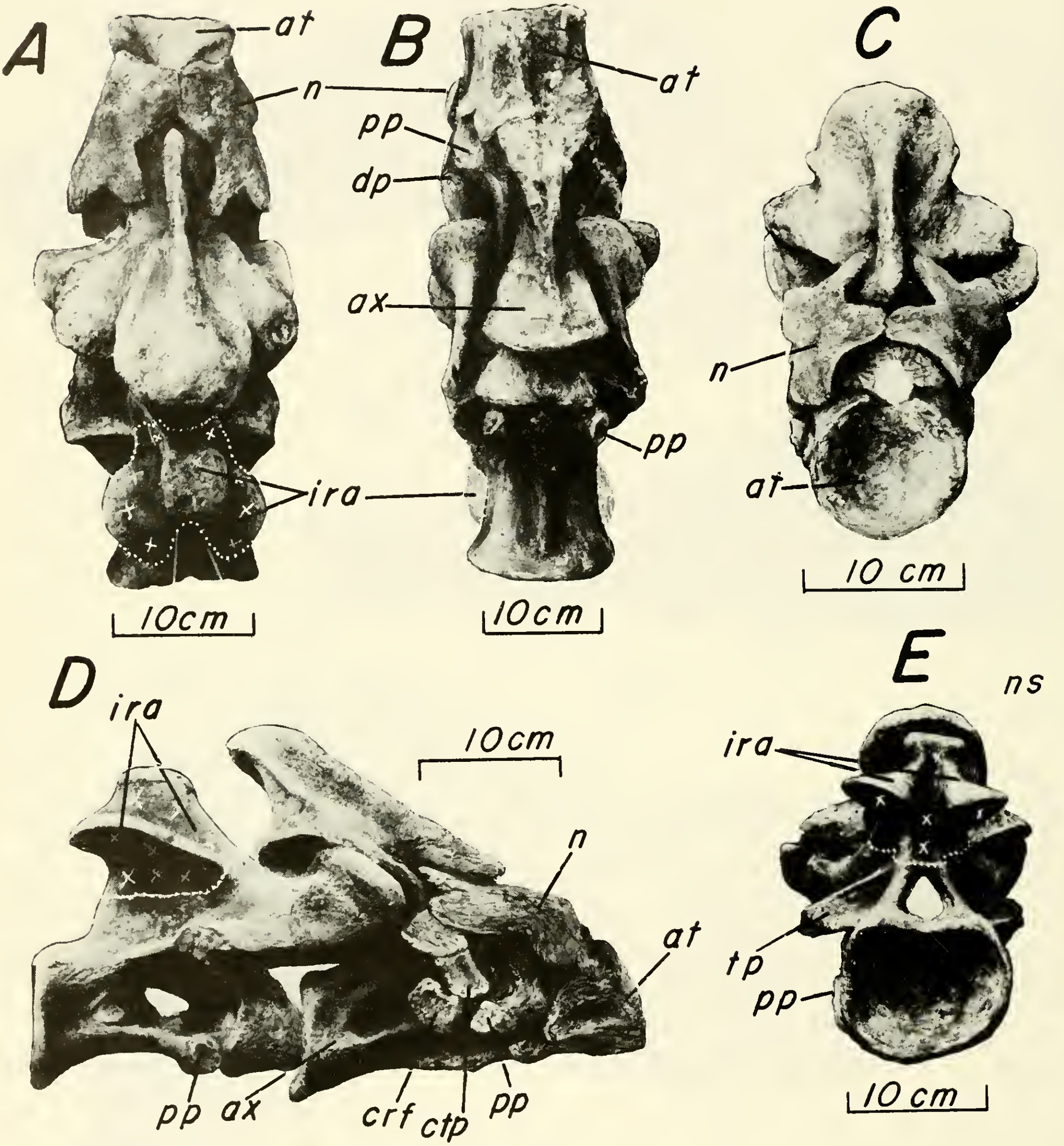

Fig. 10. Potter Creek Quarry, unidentified sauropod atlas/axis with intercentrum third cervical vertebra: A, superior view; B, inferior view; C, anterior view; D, right lateral view; E, posterior view. Abbreviations: at, atlas; ax, axis; crf, cervical rib fragment; ctp, collapsed transverse process; dp, diapophysis; ira, incorrectly restored area (x x in dotted lines); n, neurapophysis; pp, parapophysis.

spine, was readily identifiable as unrelated to *Brachiosaurus*. Because of its huge size, however, an error was made in referring it to *Ultrasaurus macintoshi* Jensen (1985), in the Brachiosauridae. To mitigate this error, I here remove the vertebra, BYU 5003, from Brachiosauridae and provisionally refer it to the Diplodocidae. This referral is based on two factors: principally, a bifurcate neural spine, and, secondly, the fact that two unusually large scapulocoracoids (Figs. 9B, 9G), found in the same (Dry Mesa) quarry, were referable to the Diplodocidae. One of these (BYU 5500, Fig. 9B) is the holotype of *Supersaurus vivianae* Jensen (1985). A large rib (Figs. 1F, 8B), though broken into many sections, appears to have been more than 3 m (over 10 ft) long.

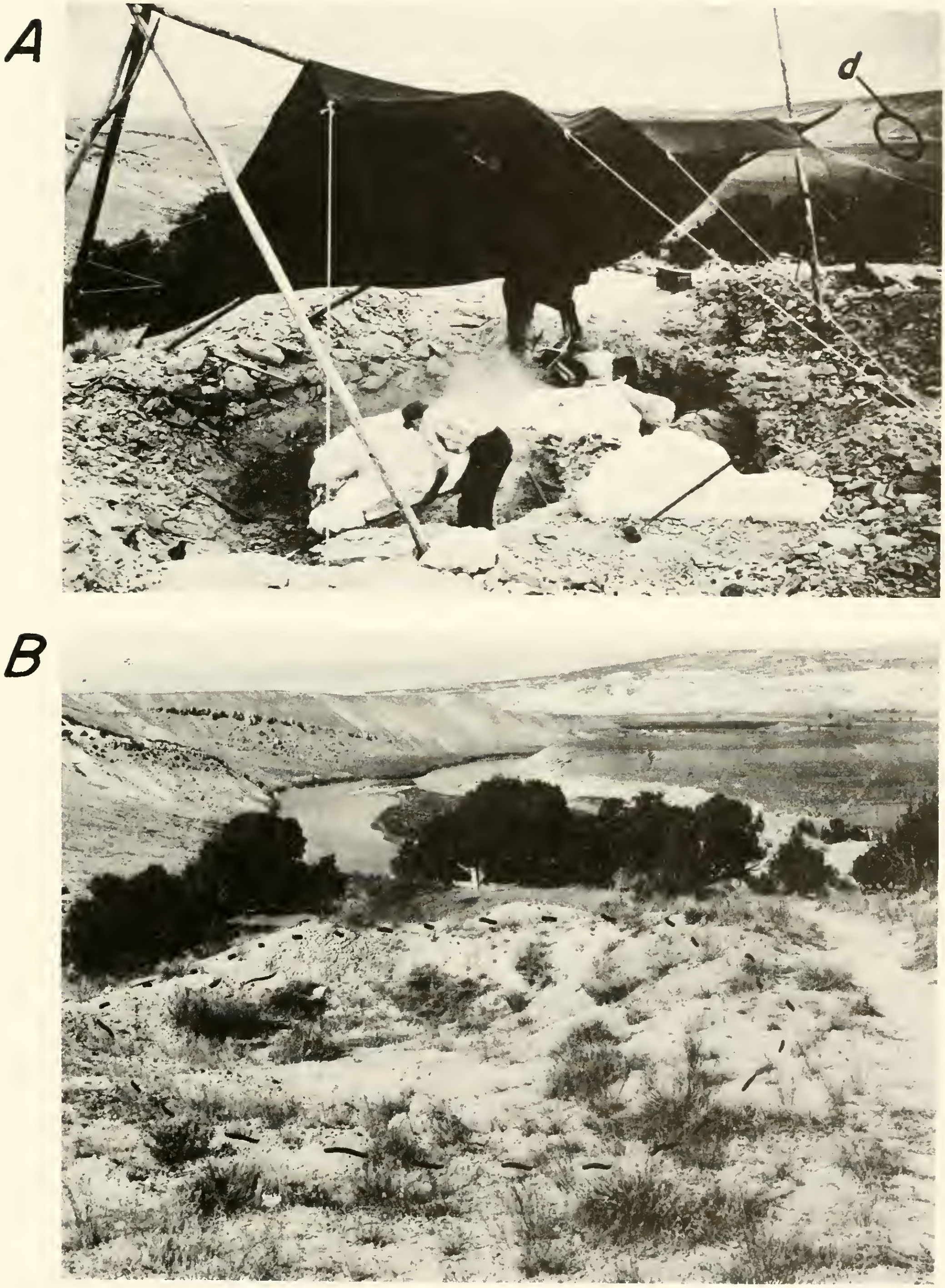

Fig. 11. Jensen/Jensen Quarry, 1966: A, Dinosaur National Monument Quarry; B, same quarry in 1986.

In 1979 a scapulocoracoid, 2.70 m (8′10″) long (Figs. 6A–B, 9I) was collected in the Dry Mesa Quarry. This scapula, BYU 5000, is readily referable to the Brachiosauridae (Fig. 9H) and is the holotype of *Ultrasaurus macintoshi* Jensen, 1985.

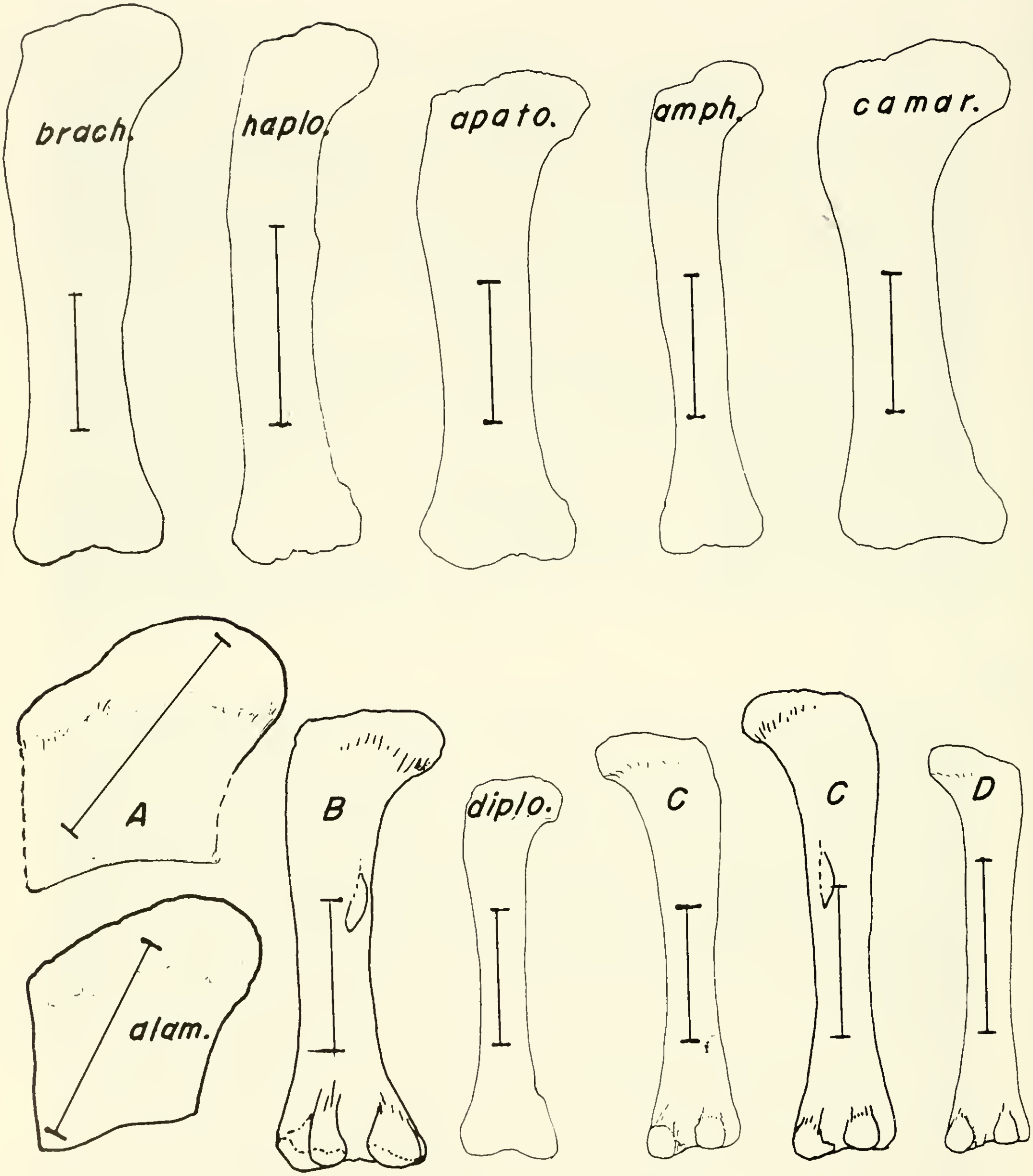

Fig. 12. Profiles of various sauropod femora: A, brachiosaurid, Recapture Creek Member, Morrison Formation; B, apatosaur; C, *Diplodocus;* D, unidentified, Dry Mesa Quarry. Abberviations: alam, alamosaur; amph, amphicoelias; apato, apatosaur; brach, brachiosaur; camar, camarasaur; diplo, *Diplodocus;* haplo, haplocanthosaur. All scale bars equal 0.5 m.

In 1985 I found the proximal third of an extremely large sauropod femur (Figs. 8A, 12A) in a uranium miner's front yard in southern Utah. The head of this femur is 1.67 m (5′6″) in circumference and was collected from the Recapture Creek Member of the Morrison Formation in Utah near the Arizona border. It is the largest bone I have ever seen; it is also the first dinosaur bone reported from the Recapture Member of the Morrison Formation and is herein pictured in Figure 8A. The proximal end of a sauropod femur is generally

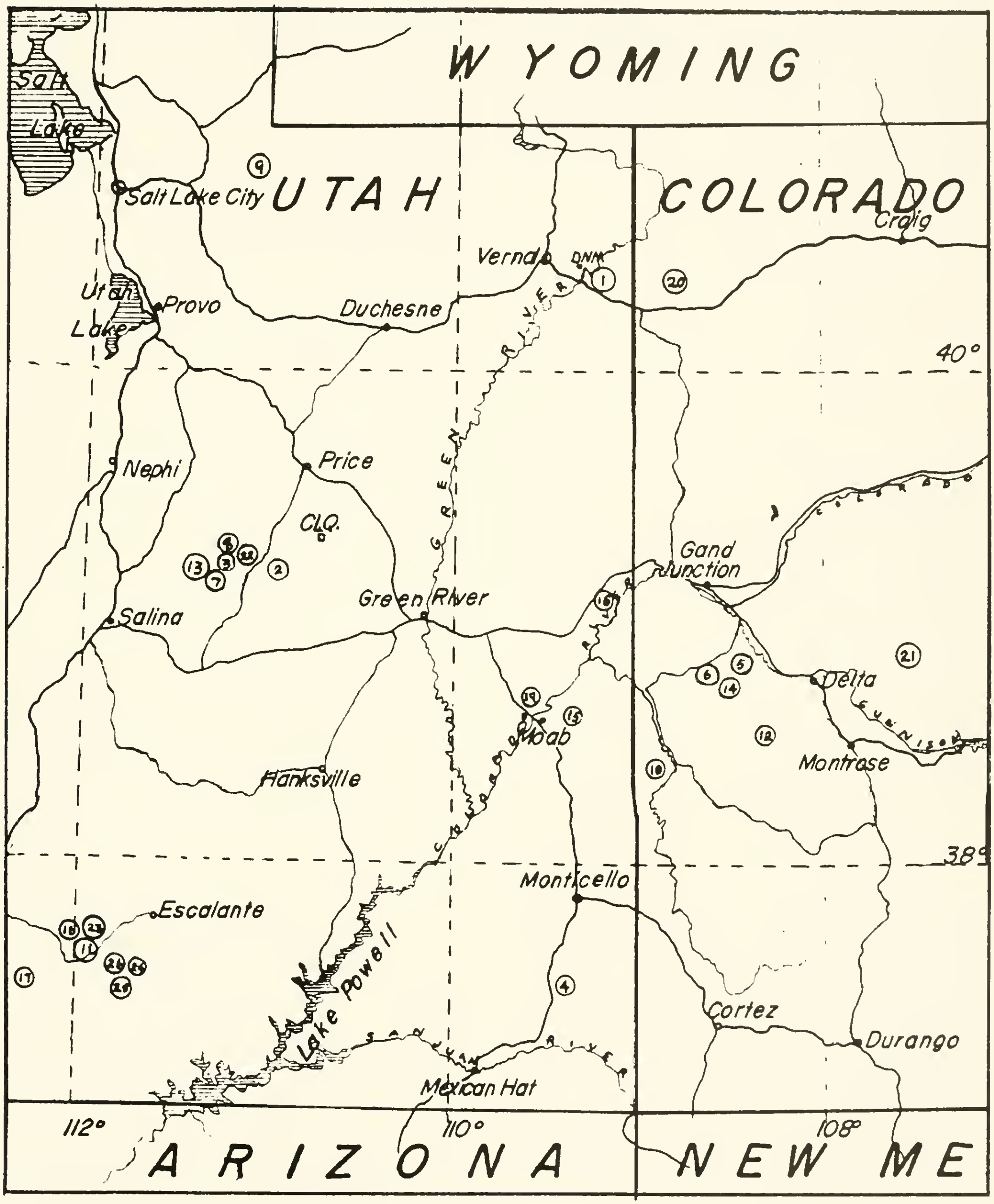
WYOMING
Salt Lake
9
Salt Lake City
UTAH
COLORADO
Craig
Vernal
DNM
1
20
GREEN RIVER
Utah Lake
Provo
Duchesne
40°
Nephi
Price
CLQ.
8
22
3
13
7
2
Gand Junction
COLORADO
Green River
16
Salina
21
6
5
14
Delta
19
15
Moab
GUNNISON
12
10
Montrose
Hanksville
38°
Monticello
Escalante
18
23
11
24
25
26
17
Lake Powell
4
Cortez
Durango
SAN JUAN RIVER
Mexican Hat
112°
110°
108°
ARIZONA
NEW ME

Fig. 13. Map of 26 quarries worked by the author in the Cretaceous and Jurassic of Utah and Colorado during a 20-year period. Name of quarry and year(s) worked, listed chronologically: 1, Jensen/Jensen, 1962, 1966; 2, Red Seeps, Easter, 1966; 3, North Horn, 1966; 4, Recapture, 1967, 1982; 5, Dominguez/Jones, 1967; 6, Cactus Park, 1968, 1977; 7, Singleton Flat, 1969; 8, Gilmore Gulley, 1969, 1980; 9, Kelvin, 1970; 10, Uravan, 1970; 11, East Fork Hadrosaur, 1971; 12, Potter Creek, 1971, 1975; 13, Gilmore Lizard, 1971; 14, Dry Mesa, 1972–1983; 15, Pterosaur Tracks, 1973; 16, Picnic Springs, 1973; 17, Navajo Hill, 1973; 18, Hinkle, 1973; 19, Dalton Well, 1975, 1978; 20, Calico Gulch, 1973, 1976; 21, Cedaredge Mosasaur, 1979; 22, Titanosaur, 1980; 23, Hummingbird, 1981; 24, Holly Hollow, 1982; 25, Faithful Smith, 1982; 26, Rotten Fuse, 1982.

not significantly diagnostic, but in profile (Fig. 12A) this specimen resembles the Upper Cretaceous *Alamosaurus* (Fig. 12 alam.) more than it does profiles of Jurassic sauropods (Fig. 12). In the latter group it bears the greatest resemblance to the profile of *Brachiosaurus* (Fig. 12 brach.) and is here referred to that family.

SYSTEMATIC PALEONTOLOGY

Suborder Sauropodomorpha

Infraorder Sauropoda

Brachiosauridae

Brachiosaurus Riggs 1903

REVISED GENERIC DIAGNOSIS.—Humerus and femur of subequal length; humerus with deltoid crest located one-third of total shaft length down from proximal end; neural arches moderately elevated, all neural spines single, not bifid, increasing in height anteriorly from sacrum to mid-dorsal region, short transverse processes on first presacral vertebra increasing in length on each vertebra to the mid-dorsal section, dorsal centra with well-developed pleurocoels, hyposphene-hypantrum articulation well developed; height of first two presacral vertebrae shorter than the preceding series, with length of centra short, length of the third to seventh presacral centra equal to half the vertebra's total height, measured from ventral border of anterior convexity to spinal apex; dorsal rib heads pneumatic; sacrum with five ilium-supporting vertebrae, width of sacrum approximately equal to length, with short sacral spines and five coossified centra; anterior caudal vertebrae with short neural spines, moderately developed caudal ribs, and no pleurocoels.

REFERRED SPECIMENS.—BYU 9754: mid-dorsal vertebra, partial left ilium, left radius, one right metacarpal, left humerus, and various rib sections, all associated.

Species Indeterminate

HORIZON AND LOCALITY.—An intermediate horizon of the Brushy Basin Member, Morrison Formation, Late Jurassic Period; Potter Creek Quarry, T49N, R12W, SW 1/4, Sec 5, Montrose County, Colorado.

COLLECTOR.—J. A. Jensen.

DESCRIPTION.—Mid-dorsal vertebra. The height of the vertebra is comparatively greater than that of the type with a proportion of centrum length to total vertebral height of 3 to 7, compared to a proportion of 3.7 to 7.2 in the type (Riggs 1904). The supraprezygopophyseal laminae are not parallel, as in *B. altithorax*, but conjoined midway up the neural spine, forming a robust pre-spinal lamina that transversely increases in width dorsally (Figs. 3D, 4A$_1$). Both diapophyses are missing, leaving the length of the transverse processes unknown. A moderately developed hyposphen-hypantrum articulation contrasts with the unusually developed intervertebral articulations in *B. altithorax*. An elongate centrum has well-developed pleurocoels. The apex of the neural spine is expanded into a robust 90-degree, transverse, gablelike metapophyseal cap (Fig. 4A$_1$). The neural arch is constricted around its base (Fig. 4A–A$_1$) rather than being anteroposteriorly long as in *Ultrasaurus* Jensen, 1985 (Fig. 4C), or long and broad as in *Dystylosaurus* Jensen, 1985 (Fig. 4B–B$_2$).

The inner and outer distal condyles of the humerus are anteriorly prominent (Fig. 5D). The rugose crest of the deltoid ridge is bulbous, comparatively short (Fig. 5B–C), and centered one-third of the total shaft length below the proximal end. A prominent, deep muscle fossa with a transverse, crenulated, lower margin (Fig. 5A) occurs in the upper part of the broad, anterior valley, adjacent to the deltoid ridge.

A metacarpal (Fig. 5E–E$_1$), probably right, MC III, has a laterally expanded distal end.

The radius (Fig. 3B), with few distinguishing features, is tentatively identified as the left.

The anterior iliac process is massive and shorter than that of *B. altithorax*. The dorsoposterior third of the ilium, including the ischiadic peduncle, is missing and is conservatively restored here after several Tendaguru brachiosaur ilia in the British Museum (Natural History) (McIntosh 1980, personal communication). The pubic peduncle is long and thin, viewed laterally, forming a weak anterior acetabular arch.

DISCUSSION.—A deep muscle fossa with a crenulated lower margin (Fig. 5A ms) occurs on the humerus in the upper part of a broad valley adjacent to the deltoid ridge, marking the terminal insertion of a large adductor cle. This may have been the "antero-superior muscle" identified in *Camarasaurus supremus* by Osborn and Mook (1921), or the M. pectoralis, or an equivalent of the M. deltoideus, said to terminate on or near the deltoid ridge in ornithischian dinosaurs (Romer 1927). This fossa is not known to be equally prominent in other sauropod genera.

The long, comparatively weak pubic peduncle of the ilium suggests the anterior end of the ilia may have been rotated ventrally around a transverse acetabular axis, similar to the 20-degree iliac rotation seen in the sauropod *Cathetosaurus lewisi* Jensen (in press). In that genus a ventral rotation of the anterior iliac processes placed a stronger, well-buttressed section of the ilia above the head of the femur. This rotation, not reported in other sauropod genera, allowed *C. lewisi* to elevate the anterior body, neck, front limbs, and thorax to a bipedal stance. A similar iliac rotation in brachiosaurs would have compensated for an elevated thorax due to their unusually long front limbs (Riggs 1903). In non-bipedal sauropods, such as the Apatosauridae, Diplodocidae, and Camarasauridae, elevation of the anterior body would have obliged the weakest cross section of the pubic peduncle to carry a major amount of body weight.

UNIDENTIFIED SAUROPOD. It is concluded here that the atlas/axis and articulated third cervical vertebrae (Fig. 10) belong to an unidentified sauropod. This determination is strengthened by the allochthonous nature of the deposit in which three families were represented; however, only mild evidence of strong, fluctuating currents, such as heavy cross-bedded sands, grits, bone abrasion, and rip-up mudclasts, was encountered during extensive excavations in the area.

An autochthonous deposit of dinosaur bones usually contains the remains of one skeleton, representing the one-time death-site burial of an individual (Dodson et al. 1980), characteristically isolated from the disruptive hydraulic forces of active channel environments. Allochthonous deposits, on the other hand, are composed of disarticulated parts of various vertebrates collected by active hydraulic forces sweeping a drainage area during an indefinite, extended period of time.

Correcting an earlier, inaccurate report on the Potter Creek fauna (Dodson et al. 1980), which listed one taxon and the pattern of bone occurrence as "isolated skeletal parts," the Potter Creek faunal list includes at least three families: two sauropodomorphs; *Brachiosaurus* sp., and an unidentified smaller sauropod; and an unusually large theropod, possibly *Torvosaurus* Galton and Jensen (1979), or a large allosaurid. Furthermore, the pattern of bone occurrence is *associated* and *articulated*, rather than "isolated," as reported, and the locality produced elements of a well-preserved flora consisting of various undescribed reproductive structures.

TAPHONOMY.—The huge brachiosaur ilium was partially destroyed, broken diagonally through its thickest section and separated from the dorsoposterior section, which was never found. This damage was not the result of levee overwash, stream abrasion, large-animal turbation, postburial pressure and faulting, nor scavengers, since no teeth marks were found in any of the bones. Also, the uncrushed, articulated, unidentified, smaller-sauropod cervical series was found adjacent to the broken ilium, undamaged by the force(s) partially destroying that huge element. The ilium was apparently broken elsewhere, the parts separated, with only one being transported to the site. Unusually strong hydraulic pressure would have been required to move such a heavy, irregular shape, but no evidence of high-energy fluvial activity was present in the surrounding sediments and so no explanation of this enigma is readily apparent.

When I first visited the locality, a considerable amount of shattered dinosaur bone, obviously belonging to a large individual, was lying on the slope below the deposit. The Jones family informed me that more was present when they discovered the site many years earlier. This lead to the conclusion that the major portion of a brachiosaur skeleton was present before erosion.

FLORA.—Considerable fossil plant material was present in an area adjacent to the quarry horizon in the form of reproductive structures. Cycadophyta seeds were common, from the family Cycadales (Chandler 1966), on fragments of macrosporophyll, including the micropyle of fertile embryos. I collected approximately one liter of these organs, as well as immature seeds of *Behuninia joannei* (Chandler 1966) and mature seeds of the Cycadophyta *Jensensispermum redmondi*

(Chandler 1966). Other reproductive structures included a cone of the gymnosperm Coniferales, family Taxodineae, *Sequoia* sp., seeds of the genus *Carpolithus* Linnaeus *incertae sedis* (Chandler 1966), and many megasporophyll fragments. This fossil plant material, a faunal list, and the information on taphonomy were available but not published in the first taphonomic report on the quarry (Dodson et al. 1980).

ACKNOWLEDGMENTS

The Daniel E. "Eddie" Jones family of Delta, Colorado, were responsible, circa 1943, for the first new brachiosaur bones found in the western hemisphere since the discovery of the type species of *Brachiosaurus* by E. S. Riggs in Colorado in 1900. Other brachiosaur bones described here, particularly those from the dry Mesa Quarry, are also the result of their extensive explorations on the Uncompahgre Upwarp in western Colorado. I thank Dr. John S. McIntosh for his encouraging support, Dr. Samuel P. Wells and Dr. James R. Jensen for criticizing the manuscript, and Dr. Stephen L. Wood, editor, *Great Basin Naturalist*, for his continuing support that has enabled me to continue publication of the results of 23 years of collecting new dinosaurs.

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SMALL-STONE CONTENT OF MIMA MOUNDS OF THE COLUMBIA PLATEAU AND ROCKY MOUNTAIN REGIONS: IMPLICATIONS FOR MOUND ORIGIN

George W. Cox[1], Christopher G. Gakahu[2], and Douglas W. Allen[1]

ABSTRACT.—Mima moundfields were investigated at the Lawrence Memorial Grassland Preserve, located on the Columbia Plateau in southern Wasco County, Oregon, and at three locations in the San Luis Valley and Sangre de Cristo Mountains, southern Colorado, to test the alternative hypotheses of mound origin by erosion, frost action, and soil translocation by geomyid pocket gophers. The concentrations of two size classes of small stones, gravel (8–15 mm diameter) and pebbles (15–50 mm diameter), were sampled along mound-to-intermound transects and at different depths within the mounds. Numbers and masses of small stones per unit soil volume increased from intermounds to mound tops at the Colorado sites and from mound edge to mound top at the Oregon site, where thin intermound soils lay directly on the weathering surface of basalt bedrock. Numbers and masses of small stones in the surface soil of mound tops were greater than or similar to concentrations in deeper layers. Mean masses of individual pebbles were greater in the intermound zone than in mound soils at the Oregon site, but did not differ along mound-intermound gradients at the Colorado sites. Ratios of gravel to pebbles varied significantly along the mound-intermound gradient at the Oregon site and at one Colorado site, being highest at mound edges or in intermounds. These observations support the hypothesis that mounds are formed by centripetal translocation of soil by geomyid pocket gophers, and are contrary to predictions based on theories assuming erosion or frost action to be the mechanism of mound formation.

In western North America, earth mounds, which reach about 25 m in diameter and 2 m in height and are commonly known as Mima mounds, occur in many locations from southern Canada to northern Mexico (Cox 1984a). The density of mounds ranges from about 1 to 3 per ha in localities in the Great Plains and to more than 50 per ha in many localities in California. The material forming these mounds consists largely of soil and small stones (up to about 50 mm in diameter) but includes few stones of larger size, although these may be abundant in intermound areas. Mounds of similar nature also have been reported in East Africa (Cox and Gakahu 1983, 1987), South Africa (Lovegrove and Siegfried 1986), and Argentina (Cox and Roig 1986).

In the interior montane region of western North America, Mima mounds occur from southern British Columbia, Canada (O. Slaymaker, personal communication), to central Sonora, Mexico (Hill 1906). They are very widespread on the Columbia Plateau of eastern Washington, north central Oregon, and southwestern Idaho (Freeman 1926, Fosberg 1965, Kaatz 1959, Malde 1961, 1964, Waters and Flagler 1929). In the Rocky Mountain region of the United States they occur in valleys and basins and on plateaus and mountain meadows from eastern Idaho and southwestern Montana south through northeastern Utah and Wyoming (R. Reider, personal communication) to Colorado (Murray 1967, Vitek 1978) and northern New Mexico (J. D. Vitek, personal communication).

Three major hypotheses have been suggested for the origin of mounds in the interior montane region of North America: (1) water erosion, (2) periglacial freeze-thaw dynamics, and (3) soil translocation by geomyid rodents.

Waters and Flagler (1929) postulated that the mounds of the Columbia Plateau resulted from the erosion of a volcanic ash layer laid down over the surface of basaltic rock, the intermound zones constituting "erosion furrows." Fosberg (1965) suggested that the stone nets often associated with Columbia Plateau mounds were formed by frost-sorting processes, and that soil material deposited over this system was eroded to leave mounds within the stone polygons. The erosional hypothesis was also supported by Knechtel (1962) and Washburn (1980).

Others have regarded the mounds, as well as the sorted stone nets often associated with them, to be a periglacial phenomenon. Kaatz

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(1959) suggested that moundfields were a thermokarst landscape, with the mounds representing the centers of former ice-wedge polygons. Malde (1961, 1964) and Brunnschweiler (1962) concluded that the mounds were formed in the late Pleistocene by processes of freeze-thaw and solifluction. In the Sangre de Cristo Mountains of southern Colorado, Frederking (1973) interpreted the mechanism of formation of mounds in lower alpine tundra areas to be frost heave, soil creep, and solifluction.

Finally, the Dalquest and Scheffer (1942) hypothesis that Mima-type mounds form by the centripetal translocation of soil resulting from outward tunneling of pocket gophers from their centers of activity has been applied to mounds of this region (Larrison 1942, Price 1949, Cox 1983a).

Cox and Gakahu (1986) derived alternative predictions of the major hypotheses of Mima mound origin. These predictions pertained to the small stone content of mound and intermound soils, and to moundfield geometry. They tested these predictions against data from four Mima moundfields in western Washington, central California, and southern California. They concluded that the results strongly supported the pocket gopher hypothesis of mound origin.

Our studies extend this test to mounds of the Columbia Plateau of eastern Oregon and to mounds of valley floors, upland mesas, and alpine tundra in southern Colorado.

PROCEDURE

Study Areas

In Oregon we investigated moundfields on and adjacent to the Lawrence Memorial Grassland Preserve (hereafter, Lawrence Preserve), a Registered National Natural Landmark owned by the Nature Conservancy, near Shaniko, southern Wasco County (44°57′N, 120°48′W). The mounded portion of this preserve is typical "biscuit scabland" (Copeland 1980) and lies at an elevation of 1,036–1,060 m on the Shaniko Plateau, formed of Columbia River basalts. The numerous Mima mounds range up to about 1 m in height and about 20 m in diameter. The mound soils are classified as Condon aeolian silt loams and the shallow intermound soils as Bakeoven residual, very cobbly loams. The climate of this region is cold and semiarid, with annual precipitation averaging 280 mm. The vegetation of the mounds is dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*), and that of the intermounds by Sandberg bluegrass (*Poa sandbergii*), scabland sagebrush (*Artemisia rigida*), bitterroot (*Lewisia rediviva*), and several species of biscuitroot (*Lomatium* spp.). The northern pocket gopher (*Thomomys talpoides*) is abundant at this site. This area was studied between 24 and 28 May 1986.

In southern Colorado three sites, all originally investigated by Vitek (1978), were studied. These sites span a wide range of altitudinal and climatic conditions. Sampling of these sites was carried out between 30 July and 4 August 1986.

The Blanca South site (37°20′N, 105°33′W) is located on the floor of the San Luis Valley, about 13 km south of the community of Blanca, Costilla County, at an elevation of 2,375 m. These mounds range from about 8.4 to 16.8 m in diameter and from 11.4 to 42.5 cm in height, and are developed on a residual sandy loam overlying extrusive basalt bedrock. The arid climate has less than 20 cm annual precipitation and is extremely cold in winter. The vegetation of the mounds is dominated by winterfat (*Eurotia lanata*) and blue grama (*Bouteloua gracilis*), with snakeweed (*Gutierrezia sarothrae*) and globemallow (*Sphaeralcea coccinea*) increasing in importance in intermound areas. The valley pocket gopher (*Thomomys bottae*) is common at this location.

The Mosca Flats site (37°46′N, 105°23′W) is located 9 km west of Red Wing, in western Huerfano County at an elevation of 2,800 m. Mounds at this location range from 8.2 to 13.0 m in diameter and from 20 to 71 cm in height. Soils are sandy loams developed on Quaternary gravels overlying Tertiary volcanics. Mean annual precipitation is probably 20–36 cm, and the vegetation of both mound and intermound areas is dominated by blue grama and pasture sagebrush (*Artemisia frigida*). The northern pocket gopher (*T. talpoides*) is abundant at this site.

The Alpine Ridge site (37°39′N, 105°29′W) lies at an elevation of 3,615 m in a saddle of the main ridge of the Sangre de Cristo Mountains on the border of Alamosa and Huerfano counties. Mounds range from 8.4 to 16.8 m in diameter and from 11.4 to 39.4 cm in height. Soils are residual sandy loams, in this case developed on Precambrian metamorphic rocks. Precipitation at this lower alpine tundra site is probably in excess of 50 cm. The vegetation of mounds and intermounds is dominated by *Kobresia myosuroides*, with plant cover in the intermounds being sparser and richer in mosses and lichens. The northern pocket gopher is abundant at this site.

Hypotheses

Based on the analysis of mound-formation hypotheses by Cox and Gakahu (1986), we postulated the following patterns for small rock content of mound and intermound soils:

EROSION HYPOTHESIS.— The concentration of both gravel and pebbles will be greater for intermound and mound edge than for mound tops because some concentration of these erosion-resistant elements should occur as the fines are removed to reduce the intermound surface level. Because the smaller gravel fraction should be carried away more than the pebble fraction by such erosion, the gravel/pebble ratio should be lower for the intermound and mound edge than for the mound top. Mean pebble mass should be least on the mound top and greatest at the mound edge and in the intermound zone.

FROST-SORTING HYPOTHESIS.—The concentration of gravel and pebbles should increase from mound centers to the center of the intermound zone because of transport of these stones to the margins of convectional cells (intermound centers). Because the larger pebbles should be moved more actively, the ratio of gravel to pebbles should be greatest on mound tops. The mean size of pebbles should also increase progressively from mound top to mound edge and intermound center.

FOSSORIAL RODENT HYPOTHESIS.—Both gravel and pebbles should be more concentrated on mound tops than at mound edges, if soil and small stones are moved moundward by animal activity and if fines are selectively returned toward the intermounds by erosion. Concentrations should also be greater at mound edges than in intermound areas, unless the intermound zone is a strong source area of weathering rock fragments. Gravel/pebble ratios should not be greatest on mound tops, however, because erosion should also tend to return more gravel than pebbles toward the intermounds. Mean pebble masses should be greater in the intermound zone than in the mounds, but values for mound edge and mound top should be similar because the major transportational bias should be exerted during movement of pebbles from intermound to mound edge.

Methods

Four (Alpine Ridge) to six (other sites) mounds were selected at each site for sampling small-stone content of mound and intermound soils. The diameters and maximum heights of these mounds were measured. These mounds were chosen because they were among the largest available and were surrounded on all sides by intermound flats. On the top of each mound, a 2-m square was marked out, with sampling locations designated at each corner. From these corner points, transects were paced outward toward the centers of the four widest intermound zones and sampling locations designated at the mound edge (0.5 m inward from the edge proper) and at a point one mound radius beyond the edge. A total of 12 locations were thus sampled for each mound. At each location, 1,980 cm^3 samples of the surface (0–10 cm) material, including stones less than 50 mm in maximum diameter, were collected. At the mound-top locations, pits were dug and similar samples taken at 30–40 cm (Colorado sites) or at 40–50 and 80–90 cm (Oregon site). Samples were dry-sieved in the field to retain all stones greater than 8 mm in minimum diameter. In the laboratory the small-stone fraction was separated into two size classes, arbitrarily termed gravel (8–15 mm) and pebbles (15–50 mm), and the numbers and masses of each of these components were determined. Because of heavy deposition of caliche in the Blanca South soil, samples of small stones were washed for 24 hr in concentrated HCl before sorting and analysis. This was done to obtain the concentration of elements influenced by the mound-forming mechanism, rather than by the pattern of caliche deposition.

At the Oregon site samples for fine textural analysis were also taken at the three sampling depths at one mound-top location on each mound. These samples were analyzed by the standard Bouyoucos technique (Cox 1985) to

TABLE 1. Characteristics of Mima mounds from which soil and small stone samples were collected in north central Oregon (southern Wasco County) and south central Colorado (San Luis Valley and Sangre de Cristo Mountains).

		Mean diameter (m)		Maximum height (m)	
Location	N	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range
OREGON					
Lawrence Preserve	6	14.73 ± 2.63	11.55–17.25	0.92 ± 0.12	0.80–1.09
COLORADO					
Blanca South	6	12.21 ± 1.90	10.00–14.60	0.25 ± 0.06	0.19–0.36
Mosca Flats	6	10.24 ± 1.49	8.50–12.35	0.34 ± 0.06	0.25–0.40
Alpine Ridge	4	11.92 ± 2.05	10.00–14.75	0.56 ± 0.13	0.40–0.70

obtain percentages of sand, silt, and clay in the 2-mm soil fraction. For the Colorado sites, soil textural data for samples collected in an earlier study were supplied by J. D. Vitek. These samples were taken from 12.7-cm-depth zones from the surface to the maximum depth of the soil at six locations along a transect crossing one mound at each site. The two end locations of each transect lay in the intermound zone and the four central locations on the mound surface. The percentages of sand, silt, and clay in the 2-mm fraction of these samples were also determined by the Bouyoucos hydrometer technique.

Data on the numbers and masses of small stones were analyzed by a three-factor ANOVA, using the BMDP8V statistical procedure (Dixon and Brown 1979). In these analyses the three classification factors were size class, mound, and location (either horizontal position along the mound-intermound gradient or depth of mound-top samples). Data on fine textural composition were tested with a single-factor ANOVA.

RESULTS

The mounds sampled at the Oregon site were greater in diameter and height than those at any of the Colorado sites (Table 1). In Colorado, mounds were lowest in elevation at the arid Blanca South site and increased in height, but not in diameter, with increasing elevation and precipitation. All mounds sampled were nearly circular in outline. Circularity ratios (r_c) were calculated from the area (a) and circumference (p) by the equation

$$r_c = 4\pi a/p^2$$

and ranged from 0.95 to 1.00.

Mounds at all sites were composed of soil containing an abundance of small stones (mostly less than 50 mm in maximum diameter). Some larger stones were also present. Most of these were 5–10 cm in maximum diameter. At the Colorado sites these were often at the mouths of deep holes dug into the mounds by badgers (*Taxidea taxus*) or coyotes (*Canis latrans*). The holes dug by these animals were often deeper than the mound height, and digging thus brought to the surface large stones from the zone beneath the mound proper. In one instance, a rock fragment 24 cm long was found in the spoil heap of a presumed badger hole. In contrast, large stones, including partially exposed boulders more than 50 cm in diameter, were common in the intermound zones of all moundfields. Samples of soil and stones less than 50 mm in maximum diameter were sometimes difficult to obtain in the intermound zones because of the high density of these large stones.

At the Lawrence Preserve, Oregon, data for variables relating to small-stone content varied significantly among the mounds sampled in almost all cases. However, several consistent patterns were noted along mound-intermound and mound-top depth gradients. Both total numbers and total masses of gravel and pebbles in the surface soil varied significantly along the mound-intermound gradient ($F_{2,10}$ = 4.7 and 37.2 for number and mass, respectively; $P < .05$ and $< .001$ for number and mass, respectively), being greatest in the shallow intermound soils (Fig. 1). Between the edges and tops of mounds, however, mean values for both number and mass increased, this increase being significant for mass ($F_{1,5} = 13.6$, $P < .05$). This increase was greater for pebbles than gravel, as indicated by a size-place interaction term ($F_{1,5} = 26.4$, $P < .01$). Total mass of small stones also varied significantly with depth at the tops of mounds ($F_{2,10} = 9.4$, $P < .01$), being less at the

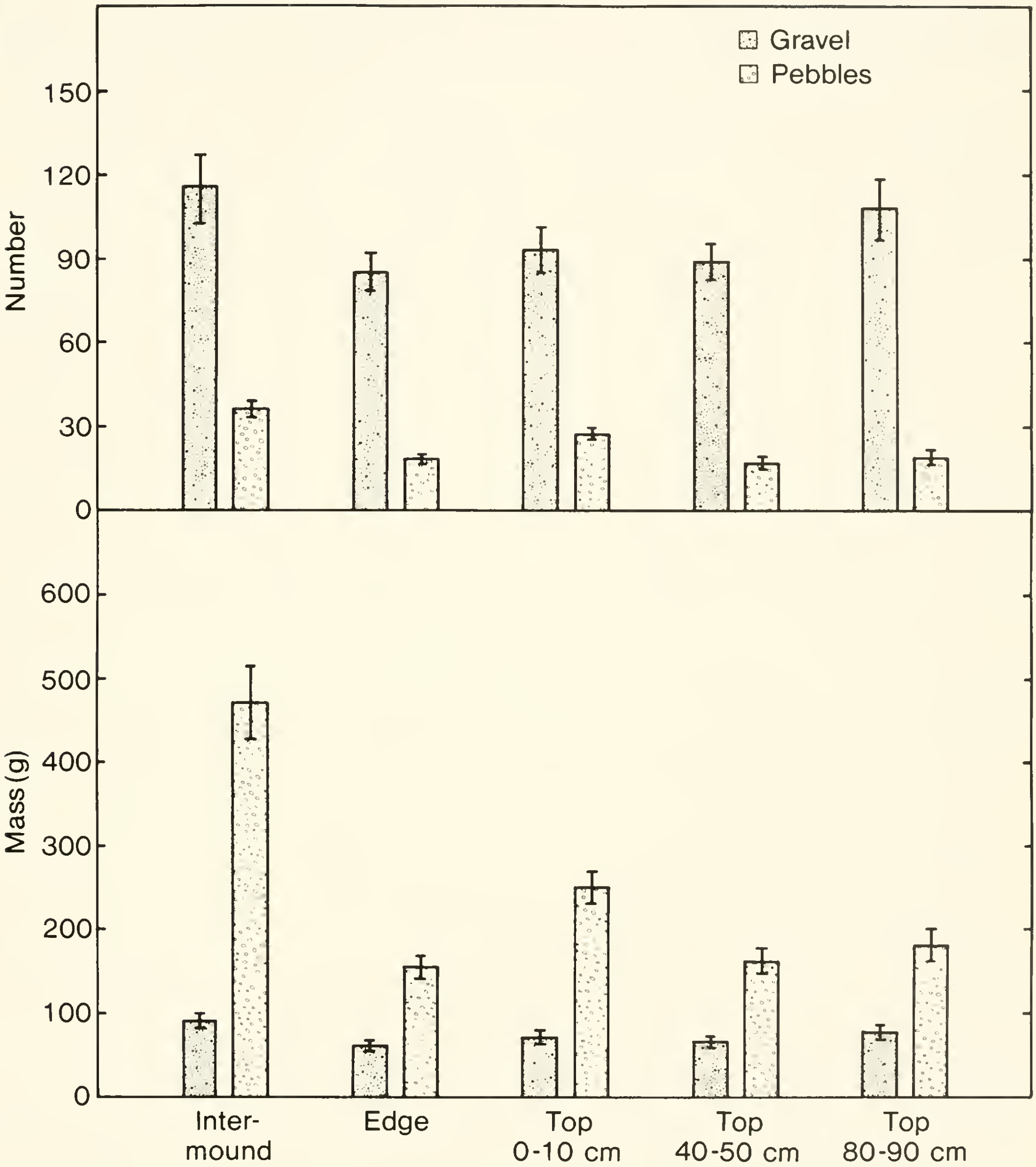

Fig. 1. Total numbers and masses of gravel and pebbles in 1,980 cm^3 soil samples from Mima mound tops (0–10, 40–50, and 80–90 cm depths), edges, and intermound zones at the Lawrence Memorial Grassland Preserve, Wasco County, Oregon. Four replicates were taken at each location on each of six mounds.

intermediate depth than at either the surface or the greatest depth. Again, this variation was more pronounced for pebbles than for gravel ($F_{2,10}$ = 18.1, $P < .001$), with pebbles showing more than a 1.5X increase in mass from intermediate depth to surface.

Ratios of gravel numbers and masses to pebble numbers and masses in the surface soil at Lawrence Preserve, Oregon (Table 2), varied significantly along the mound-intermound gradient ($F_{2,10}$ = 12.8 and 15.8 for numbers and masses, respectively; $P < .01$ and $< .001$, respectively), with the highest ratios being at the mound edge. Variation along the depth gradient at mound tops was significant only for ratios of masses ($F_{2,10}$ =

TABLE 2. Mean gravel/pebble ratios for numbers and masses and mean masses of individual gravel and pebble elements from mound and intermound sites at the Lawrence Memorial Grassland Preserve, Oregon (n = 24 in all cases).

		Gravel/pebble ratio ± SE		Mean mass (g) ± SE	
Location	Depth	Mass ratio	Number ratio	Gravel	Pebbles
Mound top	0–10 cm	0.316 ± 0.028	3.544 ± 0.244	0.792 ± 0.019	8.838 ± 0.517
Mound top	40–50 cm	0.499 ± 0.058	6.158 ± 0.586	0.758 ± 0.029	9.795 ± 0.556
Mound top	80–90 cm	0.564 ± 0.087	6.805 ± 0.806	0.724 ± 0.031	9.396 ± 0.597
Mound edge	0–10 cm	0.454 ± 0.036	5.232 ± 0.432	0.725 ± 0.023	8.575 ± 0.346
Intermound	0–10 cm	0.221 ± 0.021	3.340 ± 0.279	0.820 ± 0.027	12.837 ± 0.525

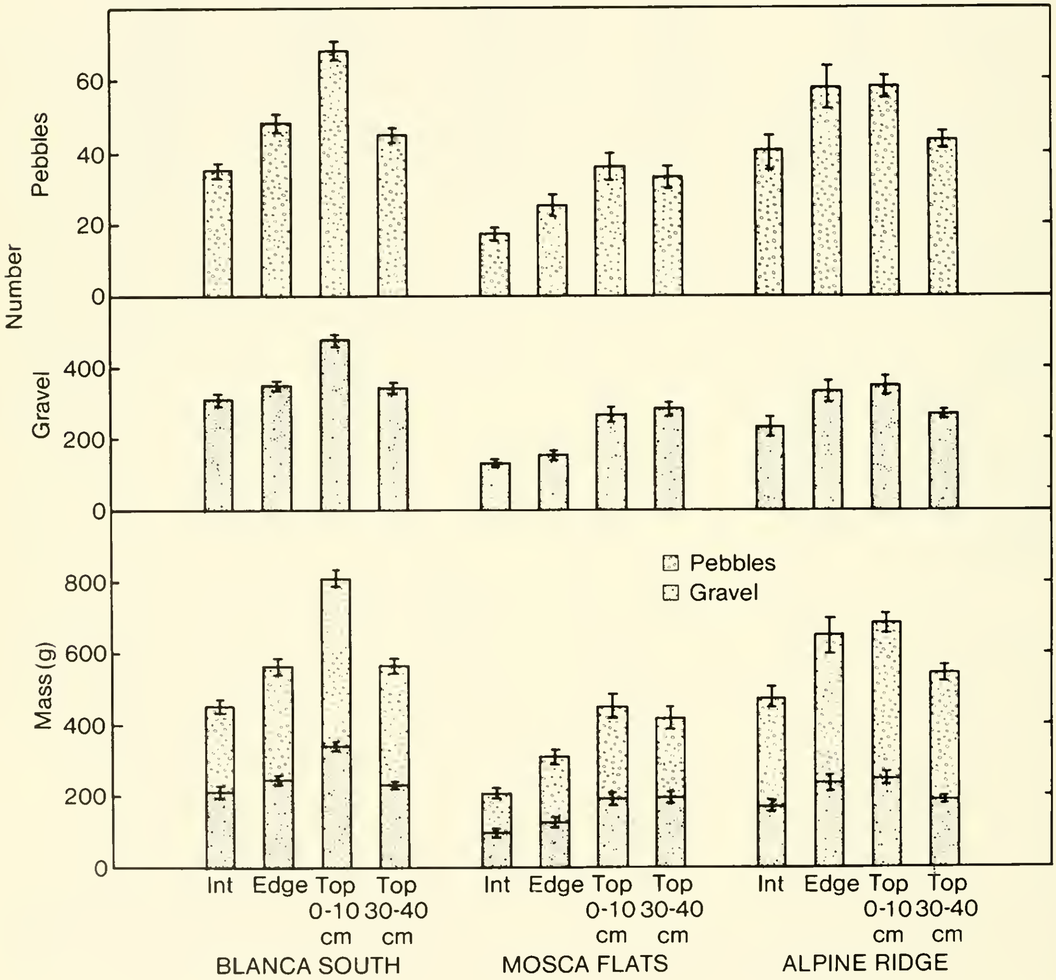

Fig. 2. Total numbers and masses of gravel and pebbles in 1,980 cm^3 soil samples from Mima mound tops (0–10 and 30–40 cm depths), edges, and intermound zones at three locations in the San Luis Valley and Sangre de Cristo Mountains of southern Colorado. Six mounds were sampled at Blanca South and Mosca Flats, four at Alpine Ridge. Four replicates were taken at each location on each mound.

6.7, P < .05), with the ratios being greatest at the deepest level.

At the Oregon site the mean mass of individual pebbles in the surface soil of intermound areas was about 1.4–1.5X that in mound soils ($F_{2,10}$ = 26.2, P < .001). No

TABLE 3. Results of ANOVA tests of variables relating to small-stone content (gravel and pebbles) of mound and intermound soils at three locations in the San Luis Valley and Sangre de Cristo Mountains, Colorado. Surface positions are mound top, mound edge, and intermound; mound-top depth positions are 0–10 and 30–40 cm. Six mounds were sampled at Blanca South and Mosca Flats, four at Alpine Ridge.

Test	Blanca South	Mosca Flats	Alpine Ridge
NUMBERS VS SURFACE POSITION			
Among places (DF = 2,10)*	F = 28.2, P < .001	F = 14.3, P < .01	F = 9.5, P < .05
Size X place (DF = 2,10)*	F = 16.1, P < .001	F = 15.2, P < .001	F = 9.3, P < .05
MASSES VS SURFACE POSITION			
Among places (DF = 2,10)*	F = 126.9, P < .001	F = 12.3, P < .01	F = 7.8, P < .05
Size X place (DF = 2,10)*	F = 4.7, P < .05	F = 4.2, P < .05	NS
NUMBERS VS DEPTH			
Among places (DF = 1,5)†	F = 89.1, P < .001	NS	NS
Size X place (DF = 1,5)†	F = 85.5, P < .001	NS	NS
MASSES VS DEPTH			
Among places (DF = 1,5)†	F = 63.7, P < .001	NS	NS
Size X place (DF = 1,5)†	NS	F = 8.8, P < .05	NS

*2,6 for Alpine Ridge
†1,3 for Alpine Ridge

TABLE 4. Ratios of gravel numbers and weights to pebble numbers and weights in soil samples from Mima mound tops (0–10 and 30–40 cm depths), edges, and intermound zones at three localities in the San Luis Valley and Sangre de Cristo Mountains, southern Colorado. Six mounds were sampled at Blanca South and Mosca Flats, four at Alpine Ridge. Values are derived from four replicates at each mound location.

		Gravel/pebble ratio			
Locality	Ratio type	Top (0–10 cm)	Top (30–40 cm)	Edge	Intermound
Blanca South (*n* = 24)	Number *	7.155 ± 0.310	8.043 ± 0.491	7.545 ± 0.436	9.216 ± 0.577
	Weight	0.756 ± 0.038	0.752 ± 0.045	0.837 ± 0.059	1.008 ± 0.105
Mosca Flats (*n* = 24)	Number	8.352 ± 0.672	9.482 ± 0.486	7.438 ± 0.412	8.749 ± 0.721
	Weight	0.950 ± 0.100	1.081 ± 0.088	0.799 ± 0.066	1.094 ± 0.116
Alpine Ridge (*n* = 16)	Number	5.922 ± 0.216	8.017 ± 1.082	5.972 ± 0.437	5.894 ± 0.566
	Weight	0.564 ± 0.024	0.553 ± 0.030	0.619 ± 0.052	0.630 ± 0.068

*DF = 3, 15, F = 2.43, P < .05

significant variation was noted with depth, however. Mean mass of individual gravel elements did not vary greatly among sampling locations.

For the Colorado sites, data on small-stone content also varied significantly among the mounds sampled for almost all variables, although less often for the Alpine Ridge site, where only four mounds were sampled. Nevertheless, clear patterns of increase in the concentration of both gravel and pebbles in the surface soil from intermound to mound top were evident at all sites, both for numbers and mass (Fig. 2). These trends were significant in all cases (Table 3) but were much stronger for the Blanca South and Mosca Flats sites than for Alpine Ridge, especially for the pebble component. Gravel and pebbles differed significantly in the strength of this trend (size × place interaction, Table 3) in all but one case (mass data, Alpine Ridge), the tendency being for pebbles to show a greater overall increase in concentration.

With only two exceptions (number and mass of gravel at Mosca Flats), mean values for concentration of gravel and pebbles were greater in the surface soil of mound tops than at a depth of 30–40 cm (Fig. 2). This tendency was significant only for Blanca South, however (Table 3).

Little significant variation of gravel/pebble ratios was noted for the Colorado sites (Table 4). Ratios of gravel and pebble numbers at Blanca South were greater in the intermounds

TABLE 5. Mean masses of individual gravel and pebbles in soil samples from Mima mound tops (0–10 and 30–40 cm depths), edges, and intermound zones at three localities in the San Luis Valley and Sangre de Cristo Mountains, southern Colorado. Six mounds were sampled at Blanca South and Mosca Flats, four at Alpine ridge. Values are derived from four replicate samples from each mound location.

		Mean mass (g) ± SE			
Locality	Rock component	Top (0–10 cm)	Top (30–40 cm)	Edge	Intermound
Blanca South (*n* = 24)	Gravel *	0.714 ± 0.008	0.684 ± 0.009	0.706 ± 0.010	0.677 ± 0.010
	Pebbles	6.866 ± 0.198	7.460 ± 0.292	6.544 ± 0.238	6.683 ± 0.330
Mosca Flats (*n* = 24)	Gravel	0.752 ± 0.056	0.684 ± 0.009	0.711 ± 0.008	0.728 ± 0.012
	Pebbles	6.673 ± 0.310	6.420 ± 0.312	7.156 ± 0.355	6.355 ± 0.347
Alpine Ridge (*n* = 16)	Gravel	0.707 ± 0.013	0.715 ± 0.009	0.718 ± 0.015	0.758 ± 0.026
	Pebbles	7.490 ± 0.205	8.084 ± 0.290	7.117 ± 0.360	7.269 ± 0.317

*DF = 3,15, F = 3.56, P < .05

TABLE 6. Soil textural data for mound depth profiles at the Lawrence Memorial Grassland Preserve, Oregon, and for mound and intermound locations at three sites in the San Luis Valley and Sangre de Cristo Mountains, southern Colorado.

		Percent of 2-mm fraction ± SE		
Location	N	Sand	Silt	Clay
LAWRENCE PRESERVE, OR				
Mound top, 0–10 cm	6	34.2 ± 3.1	43.8 ± 3.3	22.0 ± 0.3
Mound top, 30–50 cm	6	34.6 ± 3.2	41.9 ± 3.5	23.6 ± 0.5
Mound top, 80–90 cm	6	31.8 ± 3.6	45.5 ± 4.2	22.7 ± 0.8
BLANCA SOUTH, CO				
Intermound, 0–25.4 cm	4	63.6 ± 2.0	21.0 ± 1.8	15.4 ± 0.3
Mound, 0–25.4 cm	8	62.5 ± 0.6	22.2 ± 0.6	15.2 ± 0.2
Mound, 25.4–50.8 cm	6	64.3 ± 1.1	20.9 ± 1.0	14.6 ± 0.5
MOSCA FLATS, CO				
Intermound, 0–25.4 cm	2	62.5 ± 0.1	21.3 ± 1.1	16.2 ± 1.0
Mound, 0–25.4 cm	8	61.7 ± 0.6	20.3 ± 1.1	18.0 ± 0.7
Mound, 25.4–50.8 cm	4	58.8 ± 1.1	18.6 ± 0.6	22.5 ± 1.5
ALPINE RIDGE, CO				
Intermound, 0–25.4 cm	4	63.8 ± 2.0	26.0 ± 1.6	10.2 ± 0.5
Mound, 0–25.4 cm	8	75.2 ± 1.4	14.2 ± 1.3	10.7 ± 0.2
Mound, 25.4–50.8 cm	3	71.3 ± 0.6	17.9 ± 0.8	10.9 ± 0.3

and in the deep zone of the mound top than in the surface soil of the mounds. Trends in mean values of gravel/pebble ratios were generally similar for Mosca Flats and Alpine Ridge, but these patterns were not statistically significant. Mean masses of individual gravel and pebble elements showed very little variation with sampling location at any of the sites (Table 5).

Soil textural data from mound profiles at the Lawrence Preserve, Oregon, showed no consistent change with depth (Table 6), the texture being that of a loam at all levels. At the Blanca South site in Colorado no clear pattern of mound-intermound or depth variation in texture was noted. Although both mound and intermound soils were sandy loams, samples from the upslope side of the mound and the adjacent intermound were significantly sandier (n = 8, $\bar{x}$ = 64.85%) than samples from the downslope portion of the mound (n = 12, $\bar{x}$ = 61.22%; t = 4.65, P < .001). At Mosca Flats the concentration of clay in the soil varied significantly (DF = 2,11; F = 6.74, P < .025) among sampling locations, being greatest in the deeper layers of the mound. Surface soil texture at this site was also a sandy loam. At Alpine Ridge texture also varied significantly among sampling locations (DF = 2,12; F = 13.52, P < .001 for sand), the intermound soil having the highest concentration of silt and the surface soil of the mound the highest concentration of sand.

Discussion

With respect to predictions of the three hypotheses of mound origin, the trends of increase in total concentrations of gravel and pebbles from mound edge to mound top at all locations support the fossorial rodent hypothesis. The low concentrations of gravel and pebbles in intermound areas at the three Colorado sites also support this hypothesis. The very high concentrations of small rocks in the intermound areas at the Oregon site reflect only the shallowness of these soils over the weathering surface of the basalt bedrock.

The increases in small-stone concentration from deep to surface layers of the mounds at the Colorado locations likewise support the fossorial rodent hypothesis, as does the increase in mass of small rocks from intermediate depth to the surface of mounds at the Oregon site. The high surface concentrations of small stones suggest that movement of soil and small stones to the tops of mounds is being offset by erosional removal of soil fines. Thus, erosion now appears to be an agent of mound destruction.

The significantly greater change in concentration of pebbles than of gravel along the mound-intermound gradient at Lawrence Preserve, Blanca South, and Mosca Flats, together with the significant variation in the gravel/pebble number ratio at Lawrence Preserve, also supports the fossorial rodent hypothesis. In no instance, as predicted by the erosion and frost-sorting hypotheses, did the highest values of this ratio occur at mound tops. The trend of mean pebble mass at Lawrence Preserve also agrees with the prediction of the fossorial rodent hypothesis. In no case was a significant difference in mean pebble mass noted between mound top and mound edge, as predicted by the erosion and frost-sorting hypotheses.

Soil textural data from Lawrence Preserve indicate that the mound soils are very high in silt and clay content, which reflects the high loess component of the mound parent material. The lack of strong textural sorting with depth suggests that the mound soils are kept well mixed by the activities of burrowing animals. However, an argillic B horizon is evident in at least some mounds of this region (R. Reider, personal communication). Our data are very similar to those obtained by Johnson (1982) at this same site. Johnson (1982), however, noted that the intermound soils were somewhat sandier than those of the mounds. The texture of the intermound soil probably reflects the contribution of coarser components by weathering of the basaltic bedrock. At the Colorado sites texture was quite similar for both intermounds and mounds. The higher concentration of sand in mound-top soils at Alpine Ridge and the higher concentration of clay in the deeper mound soils at Mosca Flats, however, suggest that some differential removal of the finer textures occurs by wind and water erosion from the mounds.

Thus, many of the observed patterns of small-rock composition support the fossorial rodent hypothesis, and none supports the erosion or frost-sorting hypothesis. Both small-stone concentration and soil textural patterns are also consistent with the hypothesis that erosion is presently a mechanism of mound degradation rather than development.

Other evidence also argues strongly against freeze-thaw dynamics as a cause of mound formation. The suggestion that mounds may be remnant centers of ancient ice-wedge polygons (Kaatz 1959) is not supported by evidence of former permafrost, such as ice-wedge casts, from the vicinity of any present moundfield (Washburn 1980). The hypothesis that Mima mounds represent some sort of frost-sorting phenomenon is likewise not well supported by observations in any present-day periglacial environments. Most active sorted polygons lack central mounds of appreciable height and are less than 4 m in diameter (Washburn 1980). The largest sorted stone nets may reach 5–20 m in diameter and have a mounded center up to 1 m above the bordering gutter, but such nets require that the common large clasts in the soil system be 0.5–3.0 m in diameter (Goldthwaite 1976). Even these net dimensions are exceeded commonly in Mima mound fields, even though clasts of such size are rarely present. Recent models of the development of sorted polygons (Gleason et al. 1986), as well, suggest that the width of such polygons should be about 3.6X the depth of the active layer of the soil. For the very shallow soils of most Mima moundfields, this relationship does not permit the formation of mound-intermound units of the order of 20–30 m or more in diameter. Finally, even the large sorted stone circles and nets associated with Mima mounds on the Columbia Plateau have recently been attributed to the soil-mining activities of pocket gophers (Cox and Allen 1987). Thus, we conclude that periglacial hypotheses of Mima mound origin are conclusively falsified.

Data on small-stone concentrations in mound and intermound soils at these Columbia Plateau and Rocky Mountain sites are similar to those of Cox and Gakahu (1986) for sites on the Pacific Coast from southern California to the Puget Lowlands of Washington. In all, data from eight Mima mound sites, spanning a wide range of climatic and geological settings, show a consistent pattern of concentration of the small-stone fraction in mound soils. In addition, all of these sites are consistent in showing highest gravel/pebble ratios at intermound or mound edge locations, rather than on mound tops, as predicted by physical hypotheses of mound origin.

Data for the Colorado sites differ from those of the Pacific Coast sites (Cox and Gakahu 1986) and our Oregon site in showing no variation in mean pebble mass along the mound-intermound gradient. This apparently reflects the deficiency of heavy rock fragments with maximum diameters less than 50 mm in the intermound soils at the Colorado sites. Mean masses of pebbles at these locations ranged from 6.4 to 7.3 g (Table 5), compared to values of roughly 9–14 g for intermound soils at other sites.

The impetus for formation of Mima mounds by pocket gopher activity at Lawrence Preserve and Alpine Ridge sites is probably waterlogging of the shallow intermound soils during wet periods of the year. Intermound soils at these locations are shallow, and precipitation levels are high enough that wet conditions are frequent, especially in spring. In these locations, as well, water erosion probably exceeds wind erosion and may be the primary physical factor limiting height development of the mounds. Selective erosional transport of silt and clay fractions from mounds to intermounds probably accounts for the sandier texture of mound-top soils at Alpine Ridge.

The impetus for Mima mound formation at Blanca South, and perhaps Mosca Flats, must be somewhat different, however. Blanca South is the driest site at which Mima mounds have been recorded in North America. Although the mounds at this location are the lowest of those at the three Colorado sites examined in this study, they are as sharply defined and numerous as those at other Colorado sites. This suggests that the impetus for their formation is strong, but that their development in height is limited more severely by erosion. Wind erosion appears to be intense at this site, as suggested by the difference in sandiness of the upslope and downslope sides of the mound from which texture samples were obtained (Table 6).

It is unlikely that waterlogged conditions are prevalent for significant periods at the Blanca South site, which receives less than 20 cm of precipitation annually. This site possesses a thick, shallow caliche layer. In two intermound pits the surface of this layer lay at 29–36 cm. On unmounded alluvial flats immediately below the study area, rock-free, friable soil extended to a depth of 60 cm in a single test pit. Similarly, at Mosca Flats low annual precipitation and good drainage probably prevent prolonged waterlogging of the soil (J. D. Vitek, personal communication). Shallowness of the surface soil, per se, seems to favor the formation of Mima mounds at these sites. The shallowness of intermound soils may expose pocket gophers to high predation risk by animals such as badgers and coyotes, or to exposure to severe winter cold, which characterizes the San Luis Valley. Because Mima mounds are absent from shallow desert soils within the range of pocket gophers in much of the Southwest, we suggest that the primary advantage of mounds at sites on the floor of the San Luis Valley is reduction in exposure of pocket gophers to cold. In the deeper soils of mounds, these animals can locate their nests at deeper, more insulated levels.

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TYPE SPECIMENS OF RECENT MAMMALS IN THE UTAH MUSEUM OF NATURAL HISTORY, UNIVERSITY OF UTAH[1]

Eric A. Rickart[2]

ABSTRACT.—A detailed list of holotypes of Recent mammals housed in the Utah Museum of Natural History is presented.

The collection of Recent mammals at the Utah Museum of Natural History includes more than 28,500 cataloged specimens. Among these are 40 holotypes of Utah mammals deposited over a 25-year period. As part of a current project to renovate and computerize the entire mammal collection, this paper presents the first published list of type specimens.

Taxa are arranged following Hall (1981). Each entry includes the name as originally proposed, followed by the original reference and date of publication. Age, sex, nature of specimen, University of Utah (UU) catalog number, type locality, date of collection, collector(s), original number, and standard external measurements follow in order. This information was verified against previous citations (Durrant 1952, Miller and Kellogg 1955, Hall 1981) and the original specimen labels. Changes in nomenclature or taxonomic status, corrections of erroneous information, and notes on current condition of the specimen are listed under REMARKS.

LAGOMORPHA

Ochotonidae

Ochotona princeps barnsei **Durrant & Lee,** Proc. Biol. Soc. Washington 68:6, 20 May 1955. HOLOTYPE.—Adult male, skin and skull, UU 8140, from Johnson's Reservoir, 15 mi N Loa, 8,800 ft, Sevier Co., Utah; obtained 23 August 1952 by M. R. Lee, original number 123; measurements: 20-[?]-32-25.

Ochotona princeps lasalensis **Durrant & Lee,** Proc. Biol. Soc. Washington 68:4, 20 May 1955. HOLOTYPE.—Adult male, skin and skull, UU 6409, from Warner Ranger Station, La Sal Mountains, 9,750 ft, Grand Co., Utah; obtained 23 June 1948 by K. R. Kelson, original number 531; measurements: 178-6-30-23. REMARKS.—Cheek teeth loose.

Ochotona princeps wasatchensis **Durrant & Lee,** Proc. Biol. Soc. Washington 68:2, 20 May 1955. HOLOTYPE.—Adult male, skin and skull, UU 4787, from 10 mi above lower powerhouse, road to Cardiff Mine, Big Cottonwood Canyon, Salt Lake Co., Utah; obtained 24 June 1946 by J. Berryman, original number 1; measurements: 240-3-31-23, 158 g.

RODENTIA

Sciuridae

Citellus leucurus escalante **Hansen,** J. Mammal. 36:274, 26 May 1955. HOLOTYPE.—Adult female, skin and skull, UU 9195, from 2 mi SE Escalante, 5,400 ft, Garfield Co., Utah; obtained 19 August 1953 by M. R. Lee, original number 493; measurements: 225-59-40-13. REMARKS.—Placed in the genus *Ammospermophilus* (Hall 1981). Occipital and frontal regions damaged.

Citellus leucurus notom **Hansen,** J. Mammal. 36:274, 26 May 1955. HOLOTYPE.—Adult male, skin and skull, UU 9919, from Notom, Wayne Co., Utah; obtained 2 July 1936 by D. E. Beck, original number 5288N; measurements: 215-68-41-[?]. REMARKS.—Placed in the genus *Ammospermophilus* (Hall 1981). Right mandible incomplete, left zygomatic arch broken.

Citellus variegatus robustus **Durrant & Hansen,** Proc. Biol. Soc. Washington 67:264, 15 November 1954. HOLOTYPE.—Adult female, skin and skull, UU 7668, from Pass Creek, Deep Creek Mountains, 8,000 ft, Juab Co., Utah; obtained 5 June 1950 by R. M. Hansen, original number 188; measurements: 556-211-64-27. Remarks.—Placed under the name *Spermophilus* (Hall 1981).

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Sciurus aberti navajo **Durrant & Kelson,** Proc. Biol. Soc. Washington 60:79, 2 July 1947. Holotype.—Adult male, skin and skull, UU 4775, from 1 mi E Kigalia Ranger Station, 30 mi W Blanding, Natural Bridges National Monument Road, 8,000 ft, San Juan Co., Utah; obtained 10 September 1946 by G. F. Edmunds and I. B. McNulty, original number 2452 of S. D. Durrant; measurements: 486-220-74-31. Remarks.—Considered a synonym of *S. a. aberti* (Hoffmeister and Diersing, J. Mammal. 59:408, 30 May 1978).

Tamiasciurus fremonti dixiensis **Hardy,** Proc. Biol. Soc. Washington 55:87, 25 June 1942. Holotype.—Adult male, skin and skull, UU 4374, from near Further Water, Dixie National Forest, Pine Valley Mountains, ca 9,500 ft, Washington Co., Utah; obtained 23 August 1941 by O. Hall and R. Hardy, original number 2223 of Hardy; measurements: 339-131-53-28. Remarks.—Arranged as *T. hudsonicus dixiensis* (Hardy, Proc. Biol. Soc. Washington 63:13, 26 April 1950).

Glaucomys sabrinus murinauralis **Musser,** Proc. Biol. Soc. Washington 74:120, 11 August 1961. Holotype.—Adult male, skin, skull, and postcranial skeleton, UU 15652, from Timid Springs (SW 1/4, NE 1/4, Sec 7, T29S, R4W), 1 mi N Big Flat Guard Station, Tushar Mountains, 10,300 ft, Beaver Co., Utah; obtained 15 August 1960 by G. G. Musser, original number 1232; measurements: 329-155-42-30, 126 g.

Geomyidae

Thomomys talpoides durranti **Kelson,** Proc. Biol. Soc. Washington 62:143, 23 August 1949. Holotype.—Adult female, skin and skull, UU 5603, from Johnson Creek, 14 mi N Blanding, 7,500 ft, San Juan Co., Utah; obtained 20 May 1947 by K. R. Kelson, original number 201; measurements: 215-64-28-8.

Thomomys talpoides oquirrhensis **Durrant,** Bull. Univ. Utah 30(5):3, 24 October 1939. Holotype.—Adult male, skin and skull, UU 2605, from Settlement Creek, Oquirrh Mountains, 6,500 ft, Tooele Co., Utah; obtained 11 June 1938 by S. D. Durrant, original number 1461; measurements: 203-55-28-6.

Thomomys talpoides wasatchensis **Durrant,** Publ. Mus. Nat. Hist., Univ. Kansas 1:8, 15 August 1946. Holotype.—Adult male, skin and skull, UU 1604, from Midway, 5,500 ft, Wasatch Co., Utah; obtained 1 September 1936 by S. D. Durrant, original number 1049; measurements: 233-75-31-8.

Thomomys bottae bonnevillei **Durrant,** Publ. Mus. Nat. Hist., Univ. Kansas 1:41, 15 August 1946. Holotype.—Adult male, skin and skull, UU 3576, from Fish Springs, 4,400 ft, Juab Co., Utah; obtained 8 June 1940 by S. D. Durrant, original number 1955; measurements: 221-62-30-6. Remarks.—Arranged as *T. umbrinus bonnevillei* (Hall 1981).

Thomomys bottae contractus **Durrant,** Publ. Mus. Nat. Hist., Univ. Kansas 1:50, 15 August 1946. Holotype.—Adult male, skin and skull, UU 1851, from Scipio, 5,315 ft, Millard Co., Utah; obtained 17 September 1936 by S. D. Durrant, original number 1125; measurements: 255-85-33-8. Remarks.—Arranged as *T. umbrinus contractus* (Hall 1981).

Thomomys bottae convexus **Durrant,** Proc. Biol. Soc. Washington 52:159, 11 October 1939. Holotype.—Adult male, skin and skull, UU 2482, from E side Clear Lake, 4,600 ft, Millard Co., Utah; obtained 20 May 1938 by S. D. Durrant, original number 1401; measurements: 206-58-27-4. Remarks.—Arranged as *T. umbrinus convexus* (Hall 1981). Cheek teeth loose.

Thomomys bottae nesophilus **Durrant,** Bull. Univ. Utah 27(2):2, 3 October 1936. Holotype.—Adult male, skin and skull, UU 1136, from Antelope Island, Great Salt Lake, Davis Co., Utah; obtained 20 April 1935 by S. D. Durrant, original number 761; measurements: 222-60-32-6. Remarks.—Arranged as *T. umbrinus nesophilus* (Hall 1981). Left coronoid process broken.

Thomomys bottae powelli **Durrant,** Proc. Biol. Soc. Washington 68:79, 3 August 1955. Holotype.—Adult female, skin and skull, UU 7955, from Hall Ranch, Salt Gulch, 8 mi W Boulder, 6,000 ft, Garfield Co., Utah; obtained 7 August 1951 by S. D. Durrant, original number 2578; measurements: 232-65-32-5. Remarks.—Arranged as *T. umbrinus* *powelli* (Hall 1981).

Thomomys bottae robustus **Durrant**, Publ. Mus. Nat. Hist., Univ. Kansas 1:30, 15 August 1946. HOLOTYPE.—Adult male, skin and skull, UU 2726, from Orr's Ranch, Skull Valley, 4,300 ft, Tooele Co., Utah; obtained 19 June 1938 by S. D. Durrant, original number 1583; measurements: 226-65-31-5. REMARKS.—Arranged as *T. umbrinus robustus* (Hall 1981).

Thomomys bottae sevieri **Durrant**, Publ. Mus. Nat. Hist., Univ. Kansas 1:45, 15 August 1946. HOLOTYPE.—Adult female, skin and skull, UU 2530, from Swasey Spring, House Mountains, 6,500 ft, Millard Co., Utah; obtained 16 May 1938 by S. D. Durrant, original number 1380; measurements: 200-58-28-4. REMARKS.—Arranged as *T. umbrinus sevieri* (Hall 1981). Cheek teeth loose.

Thomomys bottae stansburyi **Durrant**, Publ. Mus. Nat. Hist., Univ. Kansas 1:36, 15 August 1946. HOLOTYPE.—Adult female, skin and skull, UU 2045, from South Willow Creek, Stansbury Mountains, 7,500 ft, Tooele Co., Utah; obtained 2 July 1937 by O. S. Walsh and S. D. Durrant, original number 1257 of Durrant; measurements: 209-49-28-5. REMARKS.—Arranged as *T. umbrinus stansburyi* (Hall 1981).

Thomomys bottae tivius **Durrant**, Bull. Univ. Utah 28(4):5, 18 August 1937. HOLOTYPE.—Adult female, skin and skull, UU 1827, from Oak Creek Canyon, 6 mi E Oak City, 6,000 ft, Millard Co., Utah; obtained 14 September 1936 by S. D. Durrant, original number 1100; measurements: 215-69-30-6. REMARKS.—Arranged as *T. umbrinus tivius* (Hall 1981).

Thomomys bottae wahwahensis **Durrant**, Bull. Univ. Utah 28(4):3, 18 August 1937. HOLOTYPE.—Adult male, skin and skull, UU 1750, from Wah Wah Springs, 30 mi W Milford, 6,500 ft, Beaver Co., Utah; obtained 22 July 1936 by S. D. Durrant, original number 989; measurements: 220-63-29-5. REMARKS.—Arranged as *T. umbrinus wahwahensis* (Hall 1981). Right coronoid process broken.

Heteromyidae

Perognathus parvus bullatus **Durrant & Lee**, Proc. Biol. Soc. Washington 69:183, 31 December 1956. HOLOTYPE.—Adult male, skin and skull, UU 8771, from Ekker's Ranch, Robbers Roost, 25 mi (airline) E Hanksville, 6,000 ft, Wayne Co., Utah; obtained 18 May 1951 by J. Bushman, original number 54; measurements: 160-85-22-8.

Microdipodops megacephalus leucotis **Hall & Durrant**, Murrelet 22:6, 30 April 1941. HOLOTYPE.—Adult female, skin and skull, UU 3525, from 18 mi SW Orr's Ranch, 4,400 ft, Tooele Co., Utah; obtained 6 June 1940 by S. D. Durrant, original number 1904; measurements: 142-75-24-9. REMARKS.—Bullae broken.

Dipodomys ordii celeripes **Durrant & Hall**, Mammalia 3:10, March 1939. HOLOTYPE.—Adult male, skin and skull, UU 1956, from Trout Creek, 4,600 ft, Juab Co., Utah; obtained 5 May 1937 by S. D. Durrant, original number 1168; measurements: 225-126-41-13. REMARKS.—Left bulla broken.

Dipodomys ordii cinderensis **Hardy**, Proc. Biol. Soc. Washington 57:53, 31 October 1944. HOLOTYPE.—Adult male, skin and skull, UU 4611, from sandy soil immediately north of the northern of two large cinder cones, Diamond Valley, 10 mi N St. George, Washington Co., Utah; obtained 13 February 1944 by R. Hardy, original number 2690; measurements: 232-124-38-14.

Dipodomys ordii pallidus **Durrant & Setzer**, Bull. Univ. Utah 35(26):24, 30 June 1945. HOLOTYPE.—Adult male, skin and skull, UU 3526, from Old Lincoln Highway, 18 mi SW Orr's Ranch, Skull Valley, 4,400 ft, Tooele Co., Utah; obtained 6 June 1940 by S. D. Durrant, original number 1905; measurements: 240-138-40-14. REMARKS.—Left bulla broken.

Dipodomys ordii panguitchensis **Hardy**, Proc. Biol. Soc. Washington 55:90, 25 June 1942. HOLOTYPE.—Adult male, skin and skull, UU 4375, from 1 mi S Panguitch, 6,666 ft, Garfield Co., Utah; obtained 31 August 1940 by R. Hardy, original number 2151; measurements: 257-145-41-14.

Dipodomys ordii sanrafaeli **Durrant & Setzer**, Bull. Univ. Utah 35(26):26, 30 June 1945. HOLOTYPE.—Adult female, skin and skull, UU 4612, from 1.5 mi N Price, 5,567 ft, Carbon Co., Utah; obtained 5 June 1940 by R. Hardy and H. Higgins, original number 1901 of Hardy; measurements: 249-138-42-16.

Dipodomys microps woodburyi **Hardy**, Proc. Biol. Soc. Washington 55:89, 25 June 1942. HOLOTYPE.—Adult male, skin and skull, UU 4376, from *Clistoyucca* area on Beaverdam Slope west of Beaverdam Mountains, ca 3,500 ft, Washington Co., Utah; obtained 19 October 1940 by R. Hardy, original number 2169; measurements: 302-177-43-14. Remarks.—Considered a synonym of *D. m. celsus* (Stock, J. Mammal. 51:431, 20 May 1970).

Castoridae

Castor canadensis duchesnei **Durrant & Crane,** Univ. Kansas Publ., Mus. Nat. Hist. 1:413, 24 December 1948. Holotype.—Young adult male, skin and skull, UU 4625, from Duchesne River, 10 mi NW Duchesne, 5,600 ft, Duchesne Co., Utah; obtained 23 September 1946 by D. Thomas, original number 160 of K. R. Kelson; measurements: 1176-458-165-33, 26 lbs.

Castor canadensis pallidus **Durrant & Crane,** Univ. Kansas Publ., Mus. Nat. Hist. 1:409, 24 December 1948. Holotype.—Adult female, skin and skull, UU 719, from Lynn Canyon, 7,500 ft, Box Elder Co., Utah; obtained 7 September 1932 by W. W. Newby and A. M. Woodbury, original number 762a; measurements: 1040-380-157-35.

Castor canadensis rostralis **Durrant & Crane,** Univ. Kansas Publ., Mus. Nat. Hist. 1:411, 24 December 1948. Holotype.—Young adult male, skin and skull, UU 5199, from Red Butte Canyon, Fort Douglas, 5,000 ft, Salt Lake Co., Utah; obtained 13 October 1947 by H. S. Crane and C. M. Greenhalgh, original number 446 of Crane; measurements: 1330-470-170-34.

Cricetidae

Peromyscus boylii utahensis **Durrant,** Proc. Biol. Soc. Washington 59:167, 23 December 1946. Holotype.—Adult female, skin and skull, UU 4400, from 1/2 mi above lower power station, Millcreek Canyon, 5,800 ft, Salt Lake Co., Utah, obtained 15 November 1941 by H. W. Setzer, original number 297; measurements: 188-102-20-16. Remarks.—Type locality given in original description incorrectly reads "5 miles above . . ." (Durrant 1952).

Neotoma lepida sanrafaeli **Kelson,** J. Washington Acad. Sci. 39:418, 15 December 1949. Holotype.—Adult male, skin and skull, UU 6428, from Rock Canyon Corral, 5 mi SE Valley City, 4,500 ft, Grand Co., Utah; obtained 20 June 1948 by K. R. Kelson, original number 522; measurements: 312-128-34-30. Remarks.—Hall (1981) incorrectly gives 9 January 1950 as the date of publication.

Neotoma cinerea macrodon **Kelson,** J. Washington Acad. Sci. 39:417, 15 December 1949. Holotype.—Adult male, skin and skull, UU 4725, from E side confluence Green and White rivers, 1 mi SE Ouray, 4,700 ft, Uintah Co., Utah; obtained 21 August 1946 by K. R. Kelson, original number 120; measurements: 372-158-38-36.

Microtus longicaudus incanus **Lee & Durrant,** Proc. Biol. Soc. Washington 73:168, 30 December 1960. Holotype.—Adult male, skin and skull, UU 14286, from 1/4 mi SE Burned Ridge, Mount Ellen, Henry Mountains, 10,300 ft, Garfield Co., Utah; obtained 10 September 1957 by M. R. Lee, original number 1512; measurements: 178-55-22-14.

Microtus richardsoni myodontus **Rasmussen & Chamberlain,** J. Mammal. 40:54, 20 February 1959. Holotype.—Adult male, skin and skull, UU 13084, from top of ridge, head of Boulger Canyon, 2 mi NE Huntington Reservoir, Wasatch Plateau, 10,000 ft, Sanpete Co., Utah; obtained 6 July 1956 by D. I. Rassmussen, original number 143; measurements: 231-74-25-17.

Lagurus curtatus orbitus **Dearden & Lee,** J. Mammal. 36:271, 26 May 1955. Holotype.—Adult female, skin and skull, UU 9077, from Steep Creek, 15 mi N Boulder, 8,500 ft, Garfield Co., Utah; obtained 8 July 1953 by M. R. Lee, original number 291; measurements: 133-17-16-12.

Zapodidae

Zapus princeps chrysogenys **Lee & Durrant,** Proc. Biol. Soc. Washington 73:171, 30 December 1960. Holotype.—Adult male, skin and skull, UU 13834, from 2.5 mi NE La Sal Peak, La Sal Mountains, 8,500 ft, Grand Co., Utah; obtained 17 July 1956 by M. R. Lee, original number 1436; measurements: 232-139-31-14.

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AVIAN USE OF SCORIA ROCK OUTCROPS

Mark A. Rumble[1]

ABSTRACT.—Avian use of scoria outcrop habitats was compared to use of sagebrush (*Artemisia* spp.)/grassland habitats. Outcrop habitats exhibited higher species richness, total population density, density of lark sparrows (*Chondestres grammacus*), and density of rock wrens (*Salpinctes obsoletus*). Western meadowlarks (*Sturnella neglecta*) and vesper sparrows (*Pooecetes gramineus*) were more abundant in sagebrush/grassland habitats than in scoria outcrops. Habitat relationship models indicated that the unique plant community and structural diversity provided by the scoria outcrops were correlated with increased avian use.

Because of requirements that areas surface-mined for coal and other minerals be reclaimed to the original productivity found prior to mining (e.g., Surface Mining Control and Reclamation Act 1977, numerous state laws), regulatory agencies and mining companies have sought a variety of habitat improvement techniques for reclaiming surface-mined lands for wildlife. Recently, attention has focused on the use of rocks, rock piles, and rock outcrops to enhance wildlife habitats, but little is known about the effectiveness of these or many other mitigation practices on mined lands (Evans 1982).

Scoria (fused porcellanite) outcrops occur in native sagebrush/grassland habitats throughout the Powder River Basin in northeastern Wyoming and southeastern Montana. These outcrops resulted from erosion of soil that covered burned-out coal seams near the surface. Several relatively mesic tree and shrub species are associated with these outcrops. These include ponderosa pine (*Pinus ponderosa*), juniper (*Juniperus* spp.), skunkbush sumac (*Rhus trilobata*), currant (*Ribes* spp.), and chokecherry (*Prunus virginiana*).

Increased patchiness of vegetation in shrub communities has been shown to be associated with increased numbers of avian species (Roth 1976). Rotenberry and Wiens (1980a) reported that avian abundance and species diversity in shrubsteppe communities were associated with habitat heterogeneity. Maser, Geist et al. (1979) and Maser, Thomas et al. (1979) noted the importance of rocks, cliffs, talus, outcrop, and man-made rock piles as wildlife habitat. Wiens and Rotenberry (1981) also noted a unique avifauna associated with rocky outcrops. Otherwise, little information can be found to quantify the importance of outcrop habitats to avian species.

The objectives of this study were (1) to estimate the densities of avifauna associated with scoria outcrop habitats and compare them with densities in the sagebrush/grassland habitats, and (2) to evaluate the habitat associations of the avifauna that use these habitats.

STUDY AREA AND METHODS

This study was conducted approximately 10 km north of Decker, Montana, on land under lease by the Decker Coal Company. The vegetation of the area is classified as eastern Montana ponderosa pine–savannah, which consists of scattered stands of ponderosa pine with broad expanses of northern mixed prairie (Payne 1973). Scoria outcrops were locally abundant and supported a unique plant community of relatively more mesic shrub species (Biggins et al. 1985).

Thirty-eight study sites, 19 in scoria outcrop habitats and 19 in sagebrush/grassland habitats, were located and permanently marked. Outcrop study plots were selected to represent the full range of available outcrop habitats (few to many and small to large outcrops). Sagebrush/grassland habitats were selected for similarity of vegetation to the scoria outcrop plots, ignoring the direct influences of the outcrops on vegetation. Vegetation on the sagebrush/grassland plots generally

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TABLE 1. Average (± se) densities (birds per ha) and species richness of birds occupying scoria rock outcrop and sagebrush/grassland habitats.

Species	Scoria outcrop	Sagebrush/ grassland	Significance level[a]
Lark sparrow	3.8 ± 0.4	0.2 ± 0.1	**
Western meadowlark[b]	0.3 ± <0.1	0.4 ± 0.1	*
Brewer's sparrow[b]	0.1 ± <0.1	0.2 ± 0.1	NS
Vesper sparrow[b]	<0.1 ± <0.1	0.1 ± <0.1	**
Rock wren	0.2 ± <0.1	0.0	**
Total density	5.2 ± 0.4	1.4 ± 0.2	**
Species richness	4.5 ± 0.3	3.1 ± 0.3	**

[a] *P ≤ .10, ** P ≤ .05 based on two-tailed t-test, NS not significant.

[b] Density was calculated based on the number of individuals within 50 m of the census point.

consisted of scattered sagebrush (*Artemisia tridentata* and *A. cana*) with a grass understory consisting of bluebunch wheatgrass (*Agropyron spicatum*), needle and thread (*Stipa comata*), and threadleaf sedge (*Carex filifolia*).

Avian counts were made from a variable circular plot (Reynolds et al. 1980) located at the center of each site. Birds were counted for three consecutive mornings at three-week intervals from mid-May through June 1984–85 (nine counts each year). Upon arriving at a census point, observers waited for one minute and then conducted the census for the next six minutes. Distances to birds seen or heard were estimated to the nearest m out to 30 m and to the nearest 5 m beyond 30 m. Densities of lark sparrows, rock wrens, and total birds were estimated using the Fourier series procedures described for point transects of grouped data (Burnham et al. 1980). Variance estimates were obtained indirectly (Burnham et al. 1980:54). This method of estimating variances assumes that sample points are independent. Sample points were located between 200 m and several km apart and were usually located in habitats discontinuous with the next closest sample point. Because of limited data or sighting functions that did not conform to the assumptions of line transect theory (Burnham et al. 1980), western meadowlark, vesper sparrow, and Brewer's sparrow (*Spizella breweri*) densities were estimated from the average number of individuals within 50 m of the sampling point. Density estimates from fixed radius plots assume that the probability of detection in plots equals one. This assumption was probably violated for meadowlarks.

Several methods were used to estimate habitat characteristics. Herbaceous vegetative cover was estimated by species in thirty 20 × 50-cm quadrats spaced at 1-m intervals along each of three transects radiating from the plot center (Daubenmire 1959); the starting point on each transect was selected randomly. Density of shrub species was estimated by counting all shrubs in a 50 × 50-m subplot centered over the study plots. All rocks and outcrops within a 50-m radius of the plot center and taller than 0.5 m were counted; thereafter, height, width, and length were measured to the nearest dm.

Mean densities of bird species and total birds, and species richness (number of species) were compared between outcrop and sagebrush/grassland habitats using two-tailed t-tests (Steele and Torrie 1960). Species diversity was calculated using the Shannon-Wiener method for all observations within 50 m of the census point. Similarity in abundance of avian species between outcrop and sagebrush/grassland habitats was compared using Sorenson's index. Habitat relationships were tested using stepwise forward-backward multiple regression for all species except rock wrens. The dependent variable was the estimated density of each species for a plot. Stepwise forward-backward discriminant function analysis (Nie et al. 1975) was used to evaluate rock wren habitat relationships due to the presence-absence nature of their distribution on study plots. Classification functions from discriminant analysis were evaluated using the jackknife procedure in BMDP7M (Dixon et al. 1983). The following variables were used in the habitat analyses: percentages of total vegetative cover, grasses, forbs, bare ground, litter, threadleaf sedge, bluebunch wheatgrass, cheatgrass (*Bromus* spp.), needle and thread, and cactus (*Opuntia* spp.); densities of sagebrush and skunkbush sumac; densities and

TABLE 2. Habitat variables associated with avian use of rock outcrop and sagebrush/grassland habitats near Decker, Montana.[a]

Species	Independent variables	Standardized coefficient	Percent variation explained	Correlation coefficient
Rock wren	Density of rocks > 1.0 m in height	0.61	64.0	0.71
	Avg. height of rocks	0.59	71.9	0.58
Lark sparrow	Avg. height of rocks	0.78	67.2	0.82
	% cover of cactus	−0.16	69.8	−0.37
Brewer's sparrow	Density of sagebrush	0.41	17.2	0.41
Total density	Avg. height of rocks	0.56	58.2	0.76
	% herbaceous cover	−0.20	61.9	−0.40
	Vol. of rocks > 1.0 m in height	0.23	65.3	0.60
Species richness	Vol. of rocks > 1.0 m in height	0.45	31.7	0.56
	% cover of needle and thread	−0.38	44.6	−0.52

[a]Variables were selected using stepwise forward-backward multiple regression except rock wrens for which stepwise forward-backward discriminant analysis was used.

volumes of outcrops taller than 0.5 m; and densities and volumes of outcrops taller than 1.0 m. Regression equations were limited to those variables that reduced the sums of squares significantly at $P \leq .05$, and discriminant analysis was limited to those variables that contributed at least 5% to Wilk's lambda.

RESULTS

Avian Abundance

Higher total bird densities ($P \leq .05$) and higher average species richness were found on the scoria outcrop study plots compared with the sagebrush/grassland plots (Table 1). When summed over all plots, 23 species were counted within 50 m of the census points in the outcrop plots versus 10 on the sagebrush/grassland plots. Based on Sorenson's index, there was 19% similarity in the pooled species abundance between the outcrop and sagebrush/grassland habitats. Lark sparrows made up approximately 80% of the total observations in outcrop habitats, and their density on the outcrop plots was nearly 20 times greater than in the sagebrush/grassland plots. Rock wrens were found only in the outcrop habitats, although densities were relatively low. Densities of western meadowlark were greater on the sagebrush/grassland plots than on the outcrop plots ($P \leq .10$), as were vesper sparrow densities ($P \leq .05$). Brewer's sparrow densities were higher on the sagebrush/grassland plots, but the difference was not significant ($P = .38$). Species diversity in the scoria outcrop habitats (1.83) was less than in sagebrush/grassland habitats (2.70) because of lark sparrow dominance in the former. Species evenness (Pielou 1975:15) in the outcrop habitats was 0.40 versus 0.78 in the sagebrush/grassland habitats.

Habitat Relationships

Discriminant analysis of plots with rock wrens present versus those without indicated that two variables were important in discriminating ($P \leq .01$) between the groups and accounted for 72% of the variation between groups (Table 2). Both of these variables characterized attributes of the scoria outcrops. The density of outcrops taller than 1.0 m accounted for 64% of the variation, while average height of outcrops taller than 0.5 m contributed an additional 8%. Both variables had high positive simple correlations with rock wren abundance. Classification functions correctly reclassified 92% of the study plots into the correct group; two study plots without wrens were classified as suitable habitat, and one with wrens was classified as unsuitable habitat.

Two variables, average height of rock outcrops taller than 0.5 m ($P \leq .05$) and percent cover of cactus ($P \leq .10$), explained 70% of the variation in the density of lark sparrows on study plots. Average height of rocks was positively associated with the density of lark sparrows; cactus was negatively associated with lark sparrow density. Only one variable, sagebrush density, contributed significantly ($P \leq$

.05) to the reduction in the sums of squares (17%) of Brewer's sparrow densities on the study plots.

Three variables, average height of outcrops, percent total herbaceous cover ($P \leq .05$), and volume of outcrops taller than 1.0 m ($P \leq .10$), were entered into the model for total avian density on study plots. Average height of the outcrops was positively associated with total avian density and was entered first in the model, accounting for 58% of the variation in bird abundance. Total herbaceous cover, which was negatively associated with total avian density, was entered next; volume of outcrops taller than 1.0 m, which was positively associated with total density, was entered last. Each of these latter two variables added an additional 3% to the total variation accounted for by the model.

Volume of outcrops taller than 1.0 m and percent cover of needle and thread explained 45% of the variation ($P \leq .05$) in species richness. Volume of the outcrops taller than 1.0 m was positively associated with species richness, while percent cover of needle-and-thread grass was negatively associated with species richness. No significant habitat relationships were found for western meadowlarks or vesper sparrows.

DISCUSSION

Scoria rock outcrops provide a unique habitat in this shrubsteppe region. Shrub species such as skunkbush sumac, chokecherry, currant, and juniper are not found except in association with the scoria outcrops in this ecosystem. The occurrence of these shrub species was probably related to shading, protection from wind, snow drift accumulation, and mulch effects of the rocks (Biggins et al. 1985).

Rock wrens, as expected, were confined to some of the scoria outcrop habitats. Some outcrop study plots did not support rock wrens, presumably because of limited foraging areas or lack of crevices for nesting. Rock wrens selected the habitats with larger outcrops. Study plots with rock wrens had an average of 9.3 outcrops per ha that were taller than 1.0 m and an average height of 0.8 m. These averages can be somewhat misleading in that plots with rock wrens generally had several outcrops 2.0 m or greater in height with numerous smaller, sometimes single, rocks. Classification of rock wren habitats, based on these criteria, suggests that all suitable habitats for rock wrens were not filled. Wiens and Rotenberry (1981) reported high variation in local avian population densities which may have indicated "unfilled" habitats. Both of the "unfilled" habitats in the present study were relatively smaller and isolated from contiguous outcrop areas and thus may not have been large enough to meet the habitat requirements of wrens. Alternatively, other parameters not measured in this study may have limited rock wren distributions (i.e., the remaining 28% of variance not accounted for by the discriminant analysis). Renaud (1979) reported rock wrens in most eroded bedrock outcrops in Saskatchewan.

Average height of outcrops and percent cover of cactus were probably not the habitat features to which lark sparrows were responding. Skunkbush sumac was closely associated with average height of outcrops ($r = .75$). In general, larger outcrops had larger sumac and other shrubs associated with them, and lark sparrows used these shrubs for perching, singing, and nesting. Skunkbush sumac was the most common shrub in the outcrop habitats, and lark sparrows showed a high positive association with sumac density ($r = .70$). Lark sparrows also used areas occupied by tall, dense sagebrush within the study area, probably because of the increased structural habitat diversity. Wiens and Rotenberry (1981) reported that lark sparrows were correlated with shrub cover, horizontal heterogeneity, and sagebrush coverage. Percent cover of cactus was greater on grassland plots and was closely associated with several variables indicative of homogeneous single-layered stands. It is doubtful that lark sparrows avoided cactus, but rather they avoided habitats of which it was indicative. Lark sparrows occurred on 29 of the 38 study plots, and regression analysis of only these plots resulted in the same variables, order of entry, and nearly the same standardized coefficients. This would suggest that although the interpretation of the regression model may be somewhat confounded, the same two variables were describing the observed use of habitats by lark sparrows.

Brewer's sparrows were associated with dense areas of sagebrush within the study area and are considered sagebrush obligates

(Braun et al. 1976, Castrale 1982). Brewer's sparrows nest off the ground under the dense canopy of sagebrush (Best 1972), and in this study dense stands of sagebrush larger than 0.5 ha usually contained at least one singing male. Other shrub species such as *Crateagus* spp., *Prunus* spp., *Amelanchier* spp., *Ceanothus velutinus*, and *Arctostophylos patula* (Johnsguard and Rickard 1957, Beaver 1976) can provide the necessary habitat requirements for Brewer's sparrows, thus demonstrating the importance of plant physiognomy rather than plant species to birds when compared across regions or habitat types. Best (1972) reported Brewer's sparrows nesting in dead sagebrush, substituting densely branched plants for the cover normally provided by live foliage. Skunkbush sumac could presumably provide nesting cover at least comparable to sagebrush killed with herbicide. However, Brewer's sparrows were rare in the outcrop habitats, possibly because spacing between sumac plants was too great. A similar segregation of habitat selection was noted by Wiens and Rotenberry (1981) for Brewer's sparrows.

Total avian density and species richness on study plots were both best modeled by positive associations with attributes of the outcrops and negative associations with habitat features characteristic of the sagebrush/grassland habitats on the study area. It was not possible to separate the effects of the shrubs and rocks in this study since the former were dependent, at least for establishment, on the latter (Biggins et al. 1985). Average height of the outcrops and volume of outcrops taller than 1.0 m were both positively correlated with abundance of sumac and currant ($r \geq .70$) on study plots. Taller and larger outcrops provide more protection from wind, greater snow accumulation on the lee side, greater surface area for runoff of rain, and a large mass to ameliorate the fluctuations in soil temperature. Total herbaceous cover and percent cover of needle-and-thread grass were higher on the sagebrush/grassland study plots and were indicative of the homogeneous, single-layered stands. Thus, the negative correlation of these variables with total avian density and species richness was probably indicative of negative relationships between lack of structural diversity and use of habitats by these bird species.

Most small birds apparently distinguish habitats on the basis of structural characteristics (Cody 1985:7). Abundance of avian species in shrubsteppe habitats has been shown to be associated with increased vertical and horizontal diversity of the habitat (Rotenberry and Wiens 1980a). Even though the species diversity in sagebrush/grassland habitats was higher because of a more even distribution of individuals, species richness was higher and positively associated with the habitat provided by the scoria outcrops and the immediate plant community. Large differences in habitat structure result in unequal species abundance and possibly a decline in species diversity (Rotenberry 1978). Rice et al. (1980), Rotenberry and Wiens (1980b), and Wiens and Rotenberry (1981) suggested that species of vegetation were more important in determining use of areas by avian species within habitat types. Within a habitat type, vegetative structural characteristics are usually provided by particular species. It was not possible to separate the effects of individual shrub species from the added structural diversity in this study. Shrub species associated with the outcrop habitats are not typical shrubsteppe species, and the surrounding sagebrush/grassland study plots did not provide similar structural diversity from which comparisons could be made between structural diversity and plant species. The results of this study indicate that at least to some extent the unique habitat provided by the scoria outcrops and the associated plant species resulted in increased species richness and total avian densities, and a different avian community during the breeding season compared with adjacent habitats.

MANAGEMENT RECOMMENDATIONS

Reclamation specialists may enhance wildlife habitats by placing suitable rocks on reclaimed mined land. While these habitats will be different from those originally on the site, it does not seem unreasonable to take advantage of opportunities to improve wildlife habitats in view of historic losses in many areas. Based on the results of this study, I recommend the following where rock piles are selected as a reclamation goal: (1) rock should be placed in piles of varying sizes up to 2 m in height; (2) rocks and rock piles should be grouped, as opposed to evenly scattered, over large areas with approximately 9.0 rock piles per ha taller than 1.0 m; (3) the minimum area to include outcrop habitats should be about 1 ha; and (4) shrub species should be planted in and around piles to encourage establishment of unique plant communities (Biggins et al. 1985).

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COLORADO GROUND BEETLES (COLEOPTERA: CARABIDAE) FROM THE ROTGER COLLECTION, UNIVERSITY OF COLORADO MUSEUM

Scott A. Elias[1]

ABSTRACT.—Ground beetles from Rotger's collection of Colorado specimens have been identified, principally by the author, and a faunal list of 161 species from 80 localities is presented. The list includes 35 species not previously recorded from Colorado. Comparisons are made with Armin's (1963) carabid list from Boulder County and the diversity of species along transects through four elevational zones from the plains to the alpine.

In 1986 the University of Colorado acquired an insect collection from the estate of the Reverend Bernard Rotger. Fr. Rotger, C.R., was a member of the order of Theatine Fathers of southern Colorado, and 19,000 specimens from his collection are now in the University of Colorado Museum. Rotger's collection of Coleoptera included 970 specimens of ground beetles (Carabidae) collected from sites in Colorado. Most of these specimens (88%) were unidentified when the museum obtained them. I have subsequently identified these specimens, and I present here a list of all the carabid species from Rotger's Colorado collection at the University of Colorado museum (Table 1). This collection comprises 161 species from 80 collecting localities in 26 Colorado counties (Table 2). Most of the collecting localities are in the southern half of the state. The sites range in elevation from 1,100 m above sea level at Rocky Ford to 3,810 m in the Blanca Mountains.

The Colorado carabid fauna is poorly known, in that the most recent published list of taxa is that of Wickham (1902). Armin's (1963) list covers only Boulder County, and Lindroth (1961–1969) gives only occasional mention of Colorado localities for various species. The list provided in Table 1 is the beginning of a modern list for the state, but it represents only one collection, and that mostly of southern Colorado specimens.

METHODS

The specimens were identified with the aid of Lindroth's (1961–1969) keys to the Carabidae of Canada and Alaska. Nearly all of Rotger's specimens were successfully identified through Lindroth's keys, but about 50 specimens did not appear to represent species treated by Lindroth. These specimens remain unidentified and are not cited in Table 1. Specimens of *Elaphrus*, identified by George Ball, were rechecked against Goulet's (1983) revision of that genus.

Some of Rotger's original locality labels included site elevations, especially his high-mountain localities. Most other locality labels had no elevation data. Wherever possible, I have provided the elevations of these localities as published in maps and gazetteers (Table 2). For some localities I could only provide rough estimates or ranges of possible elevations (e.g., localities cited from stream and river banks), and for a few localities I was unable to find any elevational citation from maps or from Gannett's (1906) state gazetteer.

For the purposes of elevational zone grouping, beetles collected below elevations of 2,000 m were designated as plains specimens. The foothills/lower montane zone was defined as greater than 2,000 m and less than 2,500 m. The subalpine zone was defined as greater than 2,500 m and less than 3,000 m. The alpine zone was defined as greater than 3,000 m.

DISCUSSION

Table 1 lists 35 species not previously cited (i.e., Wickham 1902, Lindroth 1961–1969, Armin 1963) for Colorado. Some of these species may be more common in southern Colorado, a region which has received little prior

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Table 1. List of Carabidae identified from the Rotger Collection of Colorado specimens.

Species	Collecting localities	Dates collected	Elevational range Plains	Foothills/ Lower montane	Subalpine	Alpine
Scaphinotus elevatus Fabr.	10	?		+		
Carabus serratus Say[1]	48	VI		+		
Carabus taedatus agassii LeC.	2,6,8–10,13,16,18, 30,33,34,54,60,63,79	V/2–IX/6	+	++	+	+
Calosoma obsoletum Say	31	VII		+		
Nebria arkansana Csy.	21,30,54,60	VI/7–VIII/21		+	+	
Nebria gyllenhali Schonh.[2]	3,33,63,69,76,79	V/21–VIII/16			+	+
Nebria hudsonica LeC.[2]	33,76	V/21–VI/13			+	+
Nebria metallica Fisch.*	53,79	VI/6–VIII/6			+	
Nebria obliqua LeC.[2]	14	VI	+			
Nebria obtusa LeC.[2]	17	VII/4			+	
Nebria pallipes Say*	53	VIII/6			+	
Nebria purpurata LeC.[2]	3,54,60,63	VI/18–VII/16	+		+	+
Nebria trifaria LeC.	21,37,53	VI/6–VIII/21		+	+	+
Nebria trifaria catenata Csy.[2]	21,60,76,77	V/21–VIII/21		+	+	
Opisthius richardsoni Kby.*[1]	14	VI/12	+			
Notiophilus aquaticus L.	14,63	V/12–VI/13	+			+
Notiophilus semistriatus Say	75	VII/26				+
Notiophilus simulator Fall	57	IV/20		+		
Elaphrus californicus Mannh.[3]	28,34,67	VI/8–VI/12	+	+		
Elaphrus lecontei Crotch.[3]	4	VI		+		
Loricera pilicornis F.	24,36	V	+	+		
Pasimachus elongatus LeC.	36,47,70	IV/29–IX/22	+	+		
Pasimachus obsoletus LeC.	45,80	V/10–VIII/13	+			
Clivina impressifrons LeC.*	67	VI	+			
Patrobus septentrionis Dej.	60	VII			+	
Diplous aterrimus Dej.	14,17,33,37,42,54,62, 63,67,76	V/12–VIII/14	+		+	+
Trechus apicalis Mots.*	33	VI				+
Trechus chalybeus Dej.	13,51,79	V-IX/4		+	+	
Trechus coloradensis Schaeff.	33,60,76	V/21–VI/13			+	+
Bembidion bifossulatum LeC.	24,36,71	V/3–VII/1	+	+		
Bembidion cordatum LeC.	36	V	+			
Bembidion diligens Csy.*	52,64	VI/7–IX/7	+	+		
Bembidion grapei Gyll.	79	VI			+	
Bembidion graphicum Csy.*	4,24,36,60	V/3–VI	+	+	+	
Bembidion haruspex Csy.*	2,63,68,76	V/21–VII/13			+	+
Bembidion impotens Csy.	71	X/1	+			
Bembidion incrematum LeC.*	71	X/1	+			
Bembidion levigatum Say*	73	X/4	+			
Bembidion mormon Hayw.*	24	V		+		
Bembidion nebraskense LeC.	24,52	V–IX		+		
Bembidion obscurellum Mots.	30	VII/1		+		
Bembidion patruele Dej.*	20	IV		+		
Bembidion planiusculum Mannh.	24	?		+		
Bembidion rapidum LeC.	72,73	X/1–X/4	+			
Bembidion sordidum Kby.*	52	IX/7		+		
Bembidion timidum LeC.	67,72	VI/13–X/1	+			
Bembidion versicolor LeC.	52,67	VI/13–IX/7	+	+		
Tachys anceps LeC.	64	VI/7	+			
Tachys granarius Dej.*	11,52,73	IX/7–X/4	+	+		
Pterostichus adstrictus Eschz.	6,12,23,38,39,46,47,79	IV/19–X/30	+	+	+	
Pterostichus caudicalis Say	48	V		+		
Pterostichus chalcites Say*	66	VI/12	+			
Pterostichus fatuus Mannh.*	36	IV/12	+			
Pterostichus femoralis Kby.	36,38,79	III/29–VI/16	+		+	
Pterostichus leconteianus Ltsch.	26	IV/22	+			
Pterostichus longulus LeC.[3]	32	VI/13				+
Pterostichus lucublandus Say	12	IV/21		+		

Table 1 continued.

Species	Collecting localities	Dates collected	Elevational range			
			Plains	Foothills/ Lower montane	Subalpine	Alpine
Pterostichus protractus LeC.[3]	10,16,39,79	IV/30–IX/1		+	+	
Pterostichus scitulus LeC.	20,24,56	IV–IX/7	+	+		
Pterostichus surgens LeC.	33,39,51,63,76,79	IV/30–IX/4			+	+
Pterostichus torvus LeC.	7,40,43,72	III/29–X/1	+			
Calathus advena LeC.[3]	37,62,76,78	V/20–VI/16			+	+
Calathus ingratus Dej.[1]	63	VI/18				+
Calathus opaculus LeC.	40,75	III/29–VII	+			+
Synuchus dubius LeC.	24	VIII/6		+		
Agonum alceoneum Bates*[3]	15,36	IV/3–V/29	+			
Agonum californicum Dej.	22,24,39,67	V–VII/8	+	+		
Agonum corvus LeC.[3]	15,20	IV–V/3		+		
Agonum cupreum Dej.[3]	12	V/21		+		
Agonum cupripenne Say[3]	15	V/3			?	
Agonum extensicolle Say[3]	1,7,38,47,49	III/29–VIII	+	+		
Agonum ferruginosum Dej.[3]	15,33	V/3–VI/13			+	
Agonum subsericeum LeC.	24	V/12		+		
Amara aeneopolita Csy.*	68	VI/2			+	
Amara alpina Payk.	52,69	VII–IX/7		?		+
Amara carinata LeC.	38,56,71,72,73	III/29–X/4	+			
Amara coelebs Hayw.	68	VI/2			+	
Amara cf. *confusa* LeC.	68	VI/2			+	
Amara convexa LeC.	12,67,74	IV/21–VI/27	+	+		
Amara crassispina LeC.*	12,36	IV/21–IV/29	+	+		
Amara ellipsis Say*	78	V/20	?	?		
Amara erratica Dufts.	76	V/21			+	
Amara farcta LeC.	23,24,36,72	V/3–X/1	+	+		
Amara idahoana Csy.*	63,68	VI/2–VI/13			+	+
Amara impuncticollis Say	4,12,56,67,78	IV/21–VII/10	+	+	+	
Amara laevipennis Kby.*	20,74,76	IV–VI/27		+	+	
Amara latior Kby.	7,24,41,60,65,75	IX/30–X/10	+	+	+	+
Amara lunicollis Schiödte.*	12,74	IV/21–VI/27		+		
Amara obesa Say	24	VIII/6		+		
Amara patruelis Dej.	68	VI/2			+	
Amara quenseli Schonnh.	63,68	VI/20–VII/11			+	+
Amara sinuosa Csy.	68	VI/2			+	
Amara thoracica Hayw.	10,11,13,23,24	V/17–IX/19		+		
Cratacanthus dubius Beauv.	6,67	VI/12–VII/4	+	+		
Piosoma setosum LeC.	65,74	VI/27–VII/29	+	+		
Euryderus grossus Say	4,67,80	VII/7–VIII	+	+		
Harpalus amputatus Say	4,6,11,15,20,23,24,36, 56,65,72,79	IV/29–IX/19	+	+	+	
Harpalus bicolor Fabr.	67	VI/12	+			
Harpalus caliginosus Fabr.	5,36,67	V/11–VII/8	+			
Harpalus desertus LeC.	41,70	IV/30–IX/22	+			
Harpalus egregius Csy.	34	VI/8		+		
Harpalus erraticus Say	4	VII–IX		+		
Harpalus fallax LeC.	24	V/17		+		
Harpalus faunus Say	5,24	VII/6		+		
Harpalus fraternus LeC.	6,9,29,35,56	V/26–IX/7	+	+		
Harpalus fuliginosus Dufts.*	20,72,78	V/20–X/1	+	+	+	
Harpalus funerarius Csiki	56,67,70	VII/8–IX/22	+			
Harpalus herbivagus Say	50	V/19	+			
Harpalus lecontei Csy.	56	IX/7	+			
Harpalus opacipennis Hald.	1,6,12,20,24,36,58	IV–VII/30	+	+ +		
Harpalus paratus Csy.	4,56	VII–IX/7	+	+		
Harpalus pleuriticus Kby.	24	V/17		+		
Harpalus seclusus Csy.	2,6,12,16,20,24,27,30, 37,50,56,63,72,78	IV/19–X/1	+	+ +	+	+
Harpalus uteanus Csy.	12,20	IV/21		+		
Selenophorus pedicularis Dej.	2,19,46,71	V/23–VII/20	+	+		+

Table 1 continued.

Species	Collecting localities	Dates collected	Plains	Elevational range Foothills/ Lower montane	Subalpine	Alpine
Selenophorus planipennis LeC.	24,36,39,47,74	IV/30–VI/27	+	++		
Discoderus parallelus Hald.	67,71	VI/13	+			
Anisodactylus harrisi LeC.	36,48,49	IV/27–V/3	+	+		
Trichocellus cognatus Gyll.	12	IV/21		+		
Bradycellus congener LeC.	11,24	V/17–IX/19		+		
Bradycellus leconetei Csiki	12	IV/21		+		
Stenolophus anceps LeC.*	20	IV		+		
Stenolophus comma F.	20,24,36,38,67	III/24–VI	+	+		
Stenolophus conjunctus Say	6,36,49	IV/27–V/4	+	+		
Stenolophus fuscatus Dej.*	24	V		+		
Stenolophus rotundatus LeC.*	16,40	III/29–IV	+	+		
Stenolophus rontundicollis Haldem.*	12,24	V/21		+		
Stenolophus unicolor Dej.	20,24	IV–V		+		
Acupalpus indistinctus Dej.*	24,48,49	IV/27–V/17		+		
Dicaelus laevipennis LeC.	7	VIII	+			
Badister neopulchellus Lth.*	20	IV		+		
Chlaenius cordicollis Kby.*	64	VI/7	+			
Chlaenius leucoscelis Chevr.	7	VIII	+			
Chlaenius nebraskensis LeC.	15,20,24	IV–V/3		+		
Chlaenius pensylvanicus Say	24	V		+		
Chlaenius sericeus Forst.	1,48	V/6	+	+		
Chlaenius tricolor Chd.	11,24	IX/19		+		
Lebia viridis Say	10,24	V/17–IX/7		+		
Lebia vittata Fabr.	67	VI/13	+			
Apristus constrictus Csy.	64	VI/7	+			
Apristus pugetanus Csy.*	68	VI/2			+	
Microlestes linearis LeC.	52	IX/7		+		
Metabletus americanus Dej.	12,68	IV/21–VI/2		+	+	
Calleida viridis Dej.	24	VIII/6		+		
Cymindis americana Dej.	16,68	IV/19–VI/2		+	+	
Cymindis borealis LeC.	11,52,70	IX/7–IX/22	+	+		
Cymindis planipennis LeC.	52	IX/7		+		
Cymindis unicolor Kby.	27,60,68,80	VI/2–VIII/13	+	+	+	
Brachinus medius Harr.	36	V/3	+			

[1] Specimens identified by Rotger.
[2] Specimens identified by David Kavanaugh, California Academy of Sciences.
[3] Specimens identified by George Ball, University of Alberta.
*New published record for the state of Colorado.

attention, whereas others may be widely distributed in the state but simply not previously collected or identified for publication. Additional statewide collecting may clarify this situation for the species in question.

Most species in the Rotger list appear to occur within the habitat range suggested by Lindroth (1961–1969) for specimens collected in Canada, Alaska, and elsewhere in North America. The most diverse carabid fauna was identified from the foothill and lower montane forest regions (45 species, Fig. 1B). The plains zone produced 29 species, followed by the subalpine with 15 and the alpine zone with five species. Forty-six species were found in two zones, especially overlapping between the plains and foothills/lower montane zones (29 species). Seven species were found in three zones, and three species were found in all four zones.

This distribution of species through four altitudinal zones contrasts with the distribution of species through the same zones in Boulder County (Fig. 1A), as described by Armin (1963). In Armin's study the plains zone contained the most diverse carabid fauna (61 species), followed by the foothills/montane with 34 species, the subalpine with 21, and the alpine zone with only one species. Armin noted many species which occurred in two or more zones, but the patterns of zonal overlap are quite different from those in the

TABLE 2. List of collecting localities for specimens listed in Table 1.

Site and elevation	County
1. Brighton (1,520 m)	Adams
2. Blanca Mountains (3,660 m)	Alamosa
3. Blanca Mountains (3,810 m)	Alamosa
4. Great Sand Dunes Nat'l. Mon. (2,440 m)	Alamosa/Saguache
5. Archuletta County (no specific site)	Archuletta
6. Archuletta Mesa (2,500 m)	Archuletta
7. Arboles (1,830 m)	Archuletta
8. Blanca Basin (2,560 m)	Archuletta
9. Near Blanco River at Hwy. 84 (2,380 m)	Archuletta
10. Burns Canyon near Trujillo (2,040 m)	Archuletta
11. Near Chromo (2,225 m)	Archuletta
12. Devil's Creek (ca 2,130 m)	Archuletta
13. Devil's Mountain (2,740 m)	Archuletta
14. East Fork, San Juan River (ca 1,980 m)	Archuletta
15. Echo Lake	Archuletta
16. Eight Mile Fire Lookout (2,440 m)	Archuletta
17. Fish Creek (ca 2,900 m)	Archuletta
18. Four Mile Creek (ca 1,980 m)	Archuletta
19. Frances Martinez Creek (ca 2,130 m)	Archuletta
20. Lake Pagosa (2,160 m)	Archuletta
21. Little Sand Creek (ca 2,590 m)	Archuletta
22. Pagosa Junction (1,910 m)	Archuletta
23. Pagosa Springs (2,160 m)	Archuletta
24. Stevens Reservoir (2,320 m)	Archuletta
25. Rio Conejos C2	Archuletta
26. Boulder (1,660 m)	Boulder
27. Rio Conejos (ca 2,440 m)	Conejos
28. Rio San Antonio near Manassa (2,350 m)	Conejos
29. Blanca (2,360 m)	Costilla
30. Forbes Road (2,590 m)	Costilla
31. West of Jaroso (2,310 m)	Costilla
32. La Veta Pass (2,870 m)	Costilla
33. Pass Creek near La Veta Pass (ca 2,800 m)	Costilla
34. Rito Seco (ca 2,590 m)	Costilla
35. San Luis (2,430 m)	Costilla
36. Denver (1,610 m)	Denver
37. Vicinity of Ophir (2,830 m)	Dolores
38. Near Denver (1,610 m)	Douglas
39. Devil's Head Mountain (ca 2,740 m)	Douglas
40. Near Franktown (1,870 m)	Douglas
41. Near Sedalia (1,800 m)	Douglas
42. Weminuche Pass (3,240 m)	Hinsdale
43. Hwy. 10 at Cucharas River (1,890 m)	Huerfano
44. Huerfano (1,730 m)	Huerfano
45. Near Tioga (ca 1,730 m)	Huerfano
46. Golden (1,730 m)	Jefferson
47. Morrison (2,410 m)	Jefferson
48. Near Morrison (ca 2,410 m)	Jefferson
49. One mile W of Morrison (ca 2,560 m)	Jefferson
50. East of Jefferson County	?
51. Cold Water Creek (ca 2,870 m)	La Plata
52. Hersperus (2,470 m)	La Plata
53. La Plata Creek (ca 3,200 m)	La Plata
54. La Plata Mountains (ca 3,200 m)	La Plata
55. La Plata Mountains (3,200 m)	La Plata
56. La Posta (1,920 m)	La Plata
57. Vallecitos (2,340 m)	La Plata
58. Rist Canyon	Larimer
59. Pass Creek (ca 3,200 m)	Mineral
60. Wolf Creek Pass (3,200 m)	Mineral
61. Wolf Creek Pass (3,310 m)	Mineral
62. Wolf Creek Pass (3,320 m)	Mineral

Table 2 continued.

Site and elevation	County
63. Wolf Creek Pass (3,410 m)	Mineral
64. Four Corners (ca 1,520 m)	Montezuma
65. Paradox (1,610 m)	Montrose
66. La Junta (1,240 m)	Otero
67. Rocky Ford (1,270 m)	Otero
68. Park County (no specific locality)	Park
69. Mount Evans (3,810 m)	Park
70. 16 miles S of Lamar (1,100 m)	Prowers
71. Pueblo (1,430 m)	Pueblo
72. 10 miles E of Pueblo (1,420 m)	Pueblo
73. St. Charles River (ca 1,430 m)	Pueblo
74. Del Norte (2,400 m)	Rio Grande
75. Elwood Pass (3,350 m)	Rio Grande
76. Copper Gulch (ca 2,830 m)	San Juan
77. Cunningham Gulch (ca 2,740 m)	San Juan
78. Placer Gulch	San Juan
79. Vicinity of Ophir (2,830 m)	San Miguel
80. Roggen (1,430 m)	Weld

Rotger faunal list. Armin found only 16 species living both on the plains and in the foothills/montane zones, and a broader overlap of species between the montane and subalpine zones than was found in the Rotger list. Also, Armin identified 18 species living throughout four zones, compared with only three species in the Rotger list. It may be that these differences in faunal diversity along altitudinal transects represent real differences between the carabid faunas of southern and northern Colorado. On the other hand, Armin's habitat preference data may be more reliable than that derived from the Rotger list because Armin systematically collected along altitudinal transects in Boulder County through four field seasons, identifying a collection of more than 5,000 specimens, whereas Rotger's collecting appears to have been much more sporadic, with no apparent effort to collect specimens along altitudinal transects. Hence, some elevational ranges and types of habitats are poorly represented in Rotger's collection. Again, additional collecting must be done if we are to fully understand the ecological requirements and distributions of the Colorado carabid fauna.

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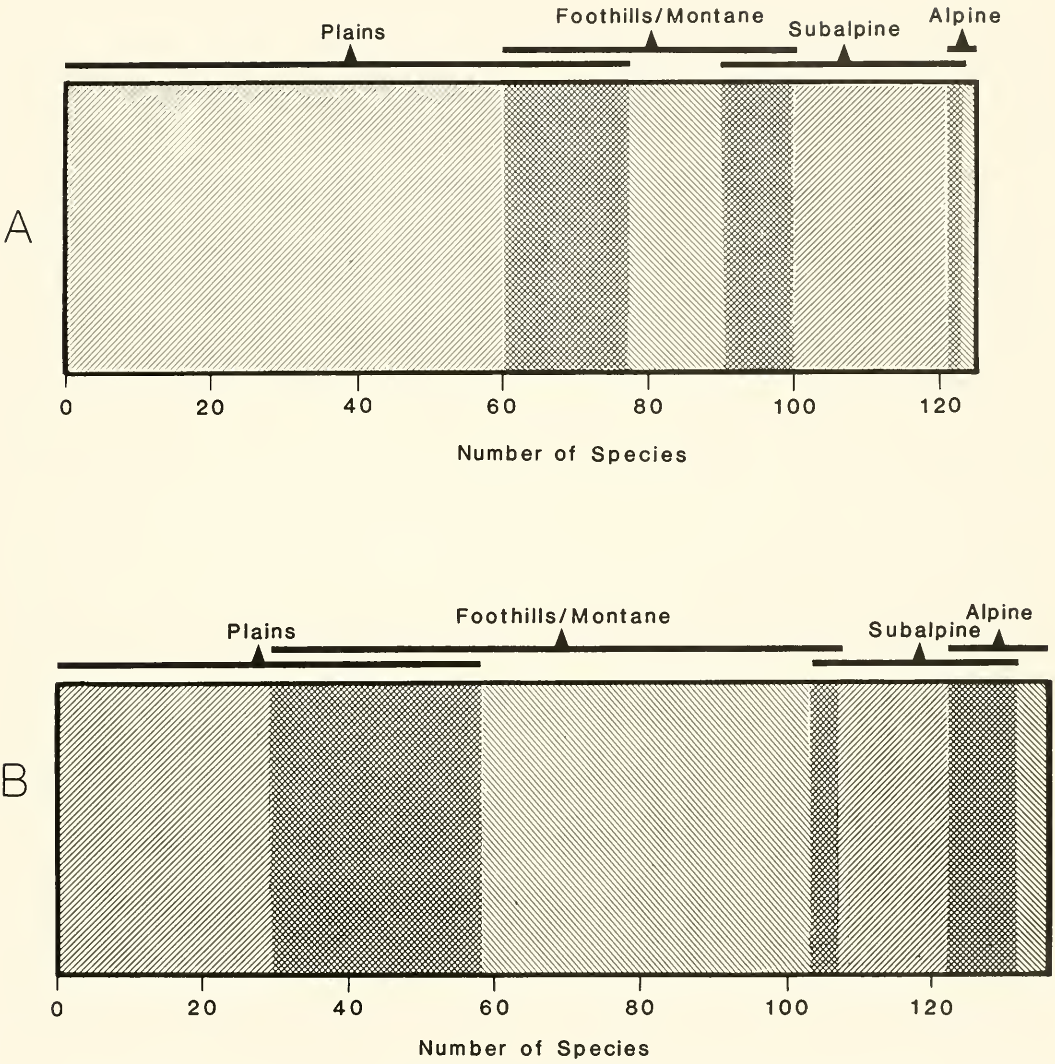

Fig. 1. Number of identified carabid species found in four elevational zones: (A) Armin (1963) in Boulder County, (B) the Rotger collection of Colorado specimens. Cross-hatched zones indicate species that overlap adjacent elevational zones. Species occupying three or more zones are excluded from the figure.

WINTER HABITAT-USE PATTERNS OF ELK, MULE DEER, AND MOOSE IN SOUTHWESTERN WYOMING

Olin O. Oedekoven[1,2] and Fredrick G. Lindzey[1]

ABSTRACT.—Habitat-use patterns of mule deer, elk, and moose were determined on two winter ranges near Kemmerer, Wyoming. Mule deer used areas with the least snow depth and dominated by sagebrush. Elk were located more often than expected on wind-swept hills but used sagebrush communities more frequently as snow depths increased. Moose were generally found associated with broad, riparian zones. All three species occasionally used the same area but differed in their use of specific vegetation types and topography.

Many winter ranges in the Rocky Mountains are used by two big game species, but few ranges support three or more species of large ungulates. Nelson (1981) suggested that although mule deer (*Odocoileus hemionus*) and elk (*Cervis elaphus*) often share winter ranges, these species compete for forage only during extreme environmental conditions. His conclusions were based on the differing foraging strategies of mule deer and elk; elk selected mostly grasses, while mule deer preferred browse species. Elk and moose (*Alces alces*) relationships on winter ranges were evaluated by Stevens (1974), Nelson (1981), and Rounds (1981). These authors concluded that because elk and moose occupied unique habitats and exhibited differing diets, they were not usually competitors. Moose and elk appear to fill two discrete ecological niches with respect to range, food habitats, physical characteristics, and social organization.

The purpose of this study was to document the winter distribution of three ungulate species on two adjacent winter ranges and to identify habitat characteristics associated with the distribution of each species.

STUDY AREAS

The study included a majority of two large, adjacent big game winter range complexes in southwestern Wyoming (Wyoming Game and Fish Department, unpublished files 1983). The two winter ranges are separated by high-elevation mountains (3,500 m) that receive little or no use by ungulates during midwinter. The combined 1985 population estimates for these areas were 20,000 mule deer, 2,700 elk, and 1,000 moose (Wyoming Game and Fish Department, unpublished files 1985).

The western wintering area is about 15 km wide by 32 km long, and the eastern area is 28 by 46 km. Drainages generally flow from the north to south and east to west within the western area and west to east within the eastern area. Western exposures dominate the western portion and eastern exposures the eastern area. Elevations vary from 2,800 m to 1,800 m. Annual precipitation ranges from 25 to 35 cm, gradually shifting to less than 25 cm in the more xeric eastern portions of the winter range. Average growing season is 60–90 days (Bureau of Land Management, Kemmerer Resource Area, unpublished files).

Sagebrush (*Artemisia* spp.) rangeland (Lanka et al. 1983) characterizes the majority of both winter ranges. This shrub vegetation type is composed of big sagebrush (*A. tridentata*), with lesser amounts of black sagebrush (*A. nova*), saltbushes (*Atriplex* spp.), and black greasewood (*Sarcobatus vermiculatus*). Mixed-shrub communities are found on more mesic sites. This community is dominated by Utah serviceberry (*Amelanchier utahensis*), western snowberry (*Symphoricarpos occidentalis*), and antelope bitterbrush (*Pursha tridentata*). Quaking aspen (*Populus tremuloides*) are present in small (< 0.5 ha) stands at higher elevations. Willow (*Salix* spp.) and grass meadows dominate the larger river bottoms. Pockets of mixed conifers dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are common on the steep, usually northern exposures of the higher-elevation ridgelines. An extensive stand of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) is present on the northwestern portion of the western winter range. Juniper (*Juniperus* spp.) stands are infrequent and limited to small (< 0.25 ha) pockets. Higher ridges that are devoid of shrubs are generally vegetated by mosses, lichens, and warm-season grasses (Poaceae).

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Most of the land in both winter ranges is administered by the Bureau of Land Management or the State of Wyoming. Principle land uses include grazing by cattle and domestic sheep and energy exploration and extraction.

METHODS

Aerial Surveys

Flights were conducted over the winter ranges during December and January of each year. A highly modified Maule N5AR single-engine, fixed-wing aircraft (Stockhill 1986) was used to fly 0.9-km-wide, established transects. Transects were located to provide complete and consistent coverage of the winter range. Animal locations were recorded on an onboard computer interfaced with an area navigational system. Locations were recorded in precise latitude and longitude coordinates as the aircraft flew over each animal group (one or more animals). This navigational system also allowed the same predetermined transects to be flown each month.

Data Collection

Vegetation type, topography, exposure, snow depth, snow cover, and animal activity were recorded for each observation. Vegetation-type categories included sage-grass, mixed shrub, aspen, willow, mountain mahogany, mixed conifer, alpine grass, and agricultural areas. Topographic categories were: drainage (draws, ditches, and narrow canyons), flat (less than 5% slope), toeslope (slope base to 30 m up a slope), steep (20+% slope), ridgeline, and hilltop. Exposure categories were one of the eight cardinal directions. Snow conditions were estimated for the area occupied by an animal group and included snow depth and percent snow cover. Estimates of snow depth were subjective and based on height of plants and animals.

Estimates of availability of the various vegetative communities, topographic, and snow-condition categories were obtained by making observations at intervals of three nautical miles during aerial surveys. Data were recorded for the availability site (about 50 × 50 m) in the same manner as that used when animals were observed. Characteristics of sites where animals were observed were compared to estimates of availability using Chi-square tests of independence (Khazanie 1979) with the Mine Tab computer program (Ryan et al. 1985). Spatial overlap of species was examined by simply comparing counts of species present in 1.6-km^2 grids. These grids were positioned on section, range, and township boundaries.

Evaluation of Potential Sampling Biases

Making inferences from observation data about dispersion or habitat-use patterns requires that several assumptions regarding animal detectability be met. Animals should be equally or proportionately detectable throughout the sampled area (species and individuals). To evaluate the possibility that deer, elk, and moose were more easily detected from the airplane when standing or bedded or in specific vegetation types, we conducted surveys on the ground after each flight. We located animals by searching with a truck or snowmobile or driving to areas where they had been observed from the airplane. Once we located an animal or group of animals, we visited them periodically through the day and noted the activity (standing or bedded) and habitat type for each animal. Observations were not begun for at least 0.5 hr after the group was first located to minimize the possibility that they were located because of their activity or the vegetation type in which they were initially found. Results of ground surveys were compared with results of the airplane transects to identify differences that would suggest differential detectability. Additionally, we searched areas on the ground for animals and their sign where no animal had been observed from the air. On five occasions we walked or drove through dense vegetation types (i.e., sagebrush draws, mountain brush stands) and attempted to count the animals present for comparison with counts made from the air.

TABLE 1. Mule deer, elk, and moose observed during aerial transects and ground surveys in southwestern Wyoming, 1984–1986.

	Aerial transects		Ground surveys	
	1984–85	1985–86	1984–85	1985–86
Mule deer	188 (2131)[a]	172 (3025)	111 (1325)	150 (1486)
Elk	90 (2455)	121 (2806)	48 (1157)	37 (1563)
Moose	98 (207)	96 (244)	15 (28)	18 (26)

[a] Number of individuals observed.

TABLE 2. Percent of mule deer, elk, and moose observations in the various vegetation categories during the winters of 1984–85 and 1985–86 and estimates of availability as determined from monthly aerial sampling.

	Mule deer		Elk		Moose		Availability
Vegetation	1984–85 (n=188)	1985–86 (n=172)	1984–85 (n=90)	1985–86 (n=121)	1984–85 (n=98)	1985–86 (n=96)	(n=724)
Sage-grass	89[a]	100[a]	73	48[a]	29[a]	9[a]	77
Mixed shrub	8	—	7	16[a]	14[a]	14[a]	8
Aspen	—	—	8[a]	2	23[a]	6	3
Willow riparian	—	—	1	6	28[a]	64[a]	4
Agriculture	—	—	—	1	—	1	1
Alpine grass/moss	—	—	8[a]	26[a]	—	—	2
Mountain mahogany	1	—	1	1	5[a]	5[a]	1
Conifer	—	—	—	—	1	1	3
Juniper	2	—	2	—	—	—	1

[a] Significant ($p < .10$) differences between proportionate use and availability.

RESULTS

Observations

Transects were flown during December and January of the 1984–85 and 1985–86 winters. Ground surveys were conducted following flights on 33 days over the two winters (Table 1). Numbers of observations are presented in Table 1.

Sampling Biases

Surveys of areas where no animals were seen from the plane indicated that few animals were not detected from the air. During five extensive searches, no animals were seen and little sign was found. The proportion of animals observed standing during two-hour daylight periods in ground and aerial surveys did not differ significantly, suggesting that animal activity did not influence detectability from the airplane (mule deer, $x^2 = 6.7$, $p > .10$, 5 df; elk, $x^2 = 4.3$, $p > .10$, 5 df, moose, $x^2 = 3.9$, $p > .10$, 5 df)·

Vegetation-use patterns identified from the air did not differ significantly from those identified from ground surveys for either elk ($x^2 = 7.6$, $p > .10$, 6 df) or moose ($x^2 = 4.8$, $p > .10$, 6 df), but slightly significant differences were found between the two samples for mule deer ($x^2 = 1.37$, $p < .10$, 6 df). Greater use of the mixed-shrub vegetation type was observed during ground surveys, suggesting that mule deer use of mixed-shrub vegetation was slightly underestimated from the air. No significant difference ($p < .10$) was detected between the ground and airplane samples for any of the species in the use of topography, exposures, or snow-conditions classes.

Habitat Use

The following analyses are based only on observations from the airplane. Results suggested that deer, elk, and moose selected specific vegetation (Table 2), topography (Table 3), exposure (Table 4), and snow-conditions (Table 5) categories. Mule deer used sagebrush vegetation extensively both winters. Conversely, moose favored aspen, willow, and mixed-shrub vegetation over the proportionally more abundant sagebrush vegetation (Table 2). Elk used the alpine grass/moss vegetation type more than expected on the basis of availability of this type (Table 1).

Mule deer typically favored drainage, flat, and ridgeline topography, and elk were most frequently observed in more irregular terrain including ridges, hilltops, and steep topography (Table 3). Although some moose were

TABLE 3. Percent of mule deer, elk, and moose observations in the various topographic categories during the winters of 1984–85 and 1985–86 and estimates of availability as determined from monthly aerial sampling.

Topography	Mule deer 1984–85 (n=188)	Mule deer 1985–86 (n=172)	Elk 1984–85 (n=90)	Elk 1985–86 (n=121)	Moose 1984–85 (n=98)	Moose 1985–86 (n=96)	Availability (n=724)
Drainage	28[a]	16[a]	14	2[a]	42[a]	11	10
Flat	29[a]	23[a]	26[a]	18[a]	23[a]	63[a]	36
Toeslope	5	8	2	1[a]	—[a]	3	6
Gentle	12[a]	16[a]	14[a]	13[a]	25	5[a]	25
Steep	6[a]	16	12	18[a]	6[a]	14	12
Ridgeline	14[a]	12[a]	21[a]	17[a]	2	3	4
Hilltop	6	9	11	31[a]	2[a]	1[a]	7

[a] Significant (p < .10) differences between proportionate use and availability

TABLE 4. Percent of mule deer, elk, and moose observations in the various exposure categories during the winters of 1984–85 and 1985–86 and estimates of availability as determined from monthly aerial sampling.

Exposure	Mule deer 1984–85 (n=188)	Mule deer 1985–86 (n=172)	Elk 1984–85 (n=90)	Elk 1985–86 (n=121)	Moose 1984–85 (n=98)	Moose 1985–86 (n=96)	Availability (n=724)
North	12	7[a]	3[a]	16	9	21	15
Northeast	3	8[a]	2	5	12[a]	15[a]	4
East	12[a]	2[a]	10[a]	23[a]	12[a]	6[a]	32
Southeast	5	—[a]	6	6	6	—	4
South	22	70[a]	15[a]	11[a]	2[a]	9[a]	24
Southwest	14[a]	1	34[a]	6	6	—	4
West	27[a]	6[a]	30[a]	5[a]	45[a]	49[a]	15
Northwest	5[a]	6[a]	—	28[a]	8[a]	—	2

[a] Significant (p < .10) differences between proportionate use and availability.

observed in upland habitats, most were found within the broad, flat, willow riparian bottoms of the more extensive riverine systems.

Mule deer were most frequently observed on southern and western exposures and tended to avoid the shaded, northern exposures (Table 4). Elk occupied a variety of exposures but tended to avoid eastern and southern exposures.

Mule deer and elk selected areas with mild snow conditions, while moose were commonly found in areas with deep snow and nearly 100% snow cover (Table 5).

Spatial Overlap

Less than 30% of the combined winter ranges was used by the three species either winter, but many areas were used by more than one species (Table 6). The greatest amount of interspecific overlap occurred during January of the first winter and December of the second winter. Occasionally, all three species were found in the same grid (1–2%).

Although two species often occupied the same grid, their use of habitats within the grids differed. Significant ($p < .10$) differences were found among the use patterns of each major habitat category (vegetation, $x^2 = 2.76$; topography, $x^2 = 13.3$; exposure, $x^2 = 127.7$).

DISCUSSION

Sampling Evaluation

The similarity of results of ground and aerial surveys does not necessarily preclude the presence of bias in the aerial sample. Differential detectability is potentially a problem in both survey methods, and thus the results of both may be similarly biased. Dense vegetation is a major factor influencing detectability (Springer 1950, LaRouche and Rausch 1974), however, and the occupied wintering areas we surveyed had little dense vegetation. Juniper woodlands were very uncommon, and conifer forests were generally at higher elevations and accompanied by deep snow that precluded much use by ungulates. The three species appeared equally detectable over the occupied wintering areas. The single exception was the reduced detectability of mule

TABLE 5. Percent of mule deer, elk, and moose observations in the various snow-condition categories during the winters of 1984–85 and 1985–86 and estimates of availability as determined from monthly aerial sampling.

	Mule deer		Elk		Moose		Availability	
Percent snow cover	1984–85 (n=188)	1985–86 (n=172)	1984–85 (n=90)	1985–86 (n=121)	1984–85 (n=98)	1985–86 (n=96)	1984–85 (n=124)	1985–86 (n=293)
Bare	—	7[a]	—	13[a]	—	—	—	2
1–25	2	1	—	1	—	—	—	2
26–50	7[a]	3	—	13[a]	—	—	1	1
51–75	34[a]	17[a]	14[a]	5	—	2[a]	3	4
76–100	57[a]	72[a]	86[a]	68[a]	100[a]	98[a]	96	91
Average snow depth								
0–15 cm	64[a]	52[a]	58	54[a]	31[a]	3[a]	51	22
16–30 cm	36	48	39	39[a]	64[a]	64[a]	34	50
31–45 cm	—	—	3[a]	6[a]	5[a]	30[a]	13	20
45–60 cm	—	—	—	1[a]	—	3	2	8

[a]Significant ($p < .10$) differences between proportionate use and availability.

TABLE 6. Animal use of 1.6-km^2 grids species during the winters of 1984–85 and 1985–86.

	1984–85		1985–86	
	Dec.	Jan.	Dec.	Jan.
Number of available grids	480	480	480	480
Number of occupied grids	127	137[a]	125	105
Percent of use by at least one species	26	29	26	22
Percent occupied by two species	10[ab]	19[a]	21[ab]	16[a]
Mule deer–elk	3[ab]	8[a]	11[b]	8
Elk–moose	4	7	6	5
Mule deer–moose	3	4	4	4
Percent occupied by three species	2	1	2	2

[a]Significant ($p < .10$) difference between months in same winter.
[b]Significant ($p < .10$) difference between month in two winters.

deer from the air when they were in mixed-shrub habitat.

Habitat Use

Mule deer, the smallest of the three species, tended to use sagebrush habitats at lower elevations in areas with the least snow cover. This pattern undoubtedly reflects the influence of snow conditions and diet. Gilbert et al. (1970) reported that mule deer were generally restricted to habitats with less than 50 cm of snow. Winter diets of mule deer are dominated by browse species including big sagebrush and antelope bitterbrush (Smith 1952, Wilkins 1957).

Elk generally occupied wind-swept ridges and hilltops vegetated by alpine grasses and moss; they moved into lower, shrub-dominated habitats only when snow cover and depth increased. Nelson and Leege (1981) reported that elk winter diets were strongly influenced by forage availability as dictated by snow conditions. Elk tended to select grasses and shift to a browse diet only when grass resources became unavailable because of deep snow cover. Beall (1974) found that elk generally foraged along the upper portions of steeper slopes where solar radiation and wind acted to reduce snow cover.

Moose appear the least influenced of the three species by deep snow because of their powerful build and large hoof size (Kelsall 1969, Coady 1974). Winter diets of moose are largely governed by the available vegetation, but, overall, moose prefer browse species such as willow, rose (*Rosa* spp.), and occasionally conifers (Peek 1974). Our results indicated that moose selected willow riparian habitats. When moose occupied the more upland sites, however, they tended to select conifer, aspen, and mixed-shrub vegetation types associated with steep, northern exposures with deeper snow cover. Snow cover on northern exposures tended to be more powdery, allowing fairly unrestricted movement by moose.

Our results suggested that although deer, elk, and moose often used the same areas, they selected differing habitats within shared areas. These patterns might be expected to change with deeper snow as suggested by Cliff (1939). The greatest spatial overlap of elk and mule deer occurred during January of the first winter and December of the second, the months with the greatest snow depths (Table 2). Because of the dominant use and availability of the sagebrush vegetation type, slightly underestimating deer use of mixed-shrub vegetation from the airplane would not demonstrably alter the results presented.

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HERBIVOROUS AND PARASITIC INSECT GUILDS ASSOCIATED WITH GREAT BASIN WILDRYE (*ELYMUS CINEREUS*) IN SOUTHERN IDAHO[1]

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Abstract.—Insects inhabiting Great Basin wildrye (*Elymus cinereus* Scribn. & Merr.) were surveyed at two sites on the Snake River Plain in southern Idaho during 1982 and 1983. Forty-six species of phytophagous insects were observed. In addition, eight parasitoid species were reared from insect hosts in the plant culms and identified. Life stage, abundance, plant part utilized, and study site were recorded for each insect species collected. Insect guilds at the two sites were compared based on species presence utilizing Sorensen's similarity index. Overall, 26 insect species were common to both sites, yielding a moderate similarity index of 0.62.

The majority of the species that constitute the wildrye herbivore guilds were oligophagous (restricted to grasses). Many of these insects feed on grain crops as well as other native and introduced grasses. The relatively high diversity of phytophages on wildrye may be due to its tall, bunchgrass growth form, its abundance within its habitat, its broad geographic range, and the large number of related species of grasses in the region.

Great Basin wildrye (*Elymus cinereus* Scribn. & Merr.) is one of the largest and most widespread native bunchgrasses in the western U.S. (Lesperance et al. 1978). It is an important component of both the salt desert shrub and sagebrush/grass ecosystems. Every spring and summer the plant produces enormous amounts of biomass that may be exploited by vertebrate and invertebrate herbivores. Much is known of wildrye's palatability and utilization by large ungulate grazers (Perry and Chapman 1974, 1975, Krall et al. 1971, Lesperance et al. 1978, Murray et al. 1978), but there has been no comprehensive study of its phytophagous insect communities. An attempt was made to partition the plant into anatomical regions and identify the associated insect herbivore guilds and their parasitoids. The impacts and diversity of these guilds are discussed.

Methods

Insects associated with Great Basin wildrye were surveyed at two sites on the Idaho Snake River Plain during 1982 and 1983. The 1.1-ha, lower-elevation (1,475 m), and drier (246 mm precipitation/yr) site was located on the Idaho National Engineering Laboratory (INEL), 10 km south of Howe, Butte Co. Wildrye occupied low, saline areas surrounded by higher ground that supported Wyoming big sagebrush (*Artemisia tridentata* subsp. *wyomingensis* Beetle). The second site was located in the north end of Craters of the Moon National Monument (CRMO), 29 km southwest of Arco at 1,817 m elevation. The precipitation is almost twice as abundant at this site (426 mm/yr). Wildrye grew on an 8.5-ha, relatively wet meadow that was surrounded by mountain big sagebrush (*Artemisia tridentata* subsp. *vaseyana* [Ryberg] Beetle).

Insects were monitored on the host plant from its three-leaf phenological stage in May through seed maturation in late August. Fifteen plants were randomly selected along two random, 50-m transects at each site at weekly intervals. The insect fauna on each host plant was observed for five minutes. Insect life stage, behavior, relative abundance, and plant parts utilized were recorded. Insects were hand-picked or aspirated from the grass for later identification. Presence of internal feeders was determined by dissecting five tillers from each plant. Each week five plants at each site were excavated, examined for root- and root-crown–infesting insects, and placed into Berlese funnels to collect the resident insects.

Insect feeding was determined by direct observation such as mouthpart insertion and plant damage. While not absolutely definitive in all cases, this method is more accurate than previous sweep-net sampling programs

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(Horning and Barr 1968).

RESULTS AND DISCUSSION

Forty-six insect species in 22 families and seven orders were identified as feeding on wildrye. Each species was categorized as to abundance, life-stage feeding on wildrye, region of the host plant utilized, and host specificity (Table 1). Eight species of parasitoids were also reared from insect hosts in the culms and identified (Table 2). The host plant was partitioned into five anatomical components: roots, culms, leaves, flowers, and seeds. Each region supported a variety of insect species that employed different feeding strategies. Many of the insects utilized more than one plant part and thus were identified in more than one guild.

Root-Feeders

Aphids, mealybugs, and beetle larvae were the most abundant insects feeding on wildrye roots. The aphids, *Forda marginata* and *F. olivacea*, were collected in low numbers in the spring and early summer. Both species have been reported to feed only on grass roots and are associated with ant nests (Gillette 1918, Patch 1939, Gittins et al. 1976, Smith and Parron 1978). Two pseudococcids were less frequently collected on the roots of the host plant. One, *Cryptoripersia trichura*, is known to inhabit grass roots in Arizona and New Mexico (MacGillivray 1921).

Elaterid larvae, wireworms, were very common in the soil surrounding the roots and are known as major pests of grains and range grasses. Chafer larvae, *Dichelonyx* sp., and adult weevils, *Brachyrhinus ovatus*, were found to infest Great Basin wildrye roots at CRMO. Adult billbugs, *Sphenophorous gentilis*, were very common on the seed heads of *E. cinereus* at INEL. Billbug larvae are known to feed on the roots of a variety of grasses (Asay et al. 1983, Tashiro and Personius 1970, Kamm 1969) and were believed to feed on the roots of wildrye at the study site, but could not be located. Cerambycid larvae were collected in the root masses of wildrye and identified to the subfamily Lepturinae. *Cortodera barri*, a cerambycid commonly observed feeding on wildrye pollen as an adult, was the only species belonging to this subfamily found in the area. Therefore, it seems likely that the larvae belonged to this species.

Culm- and Leaf-Feeders

A large number of herbivores utilize both the culms and leaves of grasses; therefore, these two anatomical regions are discussed together. Grasshoppers are one of the most common and destructive groups of insects on western ranges (Watts et al. 1982). They are the most visible pests and have been studied more than any other graminivorous insects. Five species of acridids were collected on wildrye during the summers of 1982 and 1983. Four of these species are in the genus *Melanoplus*, with the migratory grasshopper, *M. sanguinipes*, being most abundant.

A few beetles were also found to be external chewers. Adult *Dichelonyx* fed on the host plant in July at CRMO. *Anisostena californica*, a chrysomelid, was observed feeding on wildrye leaves at both sites.

Larvae of three species of Hymenoptera fed internally in the grass culm. *Cephus cinctus* larvae tunneled down the stems consuming parenchyma and vascular tissues. Larvae eventually cut the stems and overwintered in the remaining stubs. Sawfly herbivory may impair transport of water and nutrients through the stem, thus detrimentally affecting grain production (Holmes 1977, Seamans et al. 1944). Jointworms, *Tetramesa* spp., were reared from wildrye culms. *Tetramesa* larvae fed on internal tissues. At least one species formed "bump galls" on the stem below the inflorescence. Spears and Barr (1985) reported that these larvae adversely affect the growth and reproduction of several range grasses. Dipteran larvae, probably chloropids, were also collected within the stems but could not be reared to adults.

Although injury due to defoliators is more apparent, fluid-feeding Homoptera and Hemiptera may have the greatest impact on wildrye and other native grasses (Haws 1982). By extracting plant fluids and pumping saliva into the plant, these insects remove essential plant sap and cytoplasm and may inject toxic compounds or transmit viruses. Cicadas, *Okanogana bella*, were very visible in the summer clinging to wildrye stems at CRMO. Leafhoppers and delphacids were the most common insects feeding on wildrye. Over 50 individuals of a delphacid, *Eurysa obesa*, were counted at one time on an individual

TABLE 1. Insects collected and observed feeding on Great Basin wildrye at Craters of the Moon National Monument (C) and the Idaho National Engineering Laboratory Site (I) in 1982–83.

Taxa	Life stage[a]	Plant parts[b]	Location	Host spec.[c]	Abundance[d]
ORTHOPTERA					
Acrididae					
Melanoplus bivittatus (Say)	n, a	c, l	C	p	co
Melanoplus femurrubrum (DeGeer)	n, a	c, l	C	p	co
Melanoplus foedus Scudder	n, a	c, l	C	p	un
Melanoplus sanguinipes (Fabricius)	n, a	c, l	C, I	p	co
Phoetaliotes nebrascensis (Thomas)	n, a	c, l	C	o	co
THYSANOPTERA					
Aeolothripidae					
Aeolothrips auricestus Treherne	a	f, s	C, I	p	co
Aeolothrips sp.	n, a	f, s	C, I	u	co
Thripidae					
Aptinothrips rufus (Gmelin)	a	f, l	C, I	o	co
Frankliniella occidentalis (Pergande)	n, a	f, s	C, I	p	co
Frankliniella sp.	n, a	f, s	C	u	co
Sericothrips sp.	n, a	f, s	C, I	u	co
HOMOPTERA					
Cicadidae					
Okanogana bella Davis	a	c, l	C	p	co
Cicadellidae					
Dikraneura carneola (Stal)	n, a	c, l	C, I	p	co
Hecalus viridis (Uhler)	n, a	l	I	p	co
Delphacidae					
Eurysa obesa Beamer	n, a	c, l	C, I	o	co
Aphididae					
Forda marginata (Koch)	n, a	r	I	o	un
Forda olivacea Rohwer	n, a	r	C	o	un
Pseudococcidae					
Cryptoripersia trichura (Cockerell)	n, a	r	C	o	un
Phenacoccus sp.	n, a	r	I	u	un
Trionymus smithii (Essig)	n, a	c, l	C	o	co
Eriococcidae					
Eriococcus insignis Newstead	n, a	c, l	C	o	un
HEMIPTERA					
Miridae					
Irbisia pacifica (Uhler)	n, a	c, l	C, I	o	co
Labops utahensis Slater	n, a	c, l	C	o	co
Litomeris debilis (Uhler)	n, a	c, l	C, I	o	co
Stenodema laevigatum (Linnaeus)	n, a	c, l	C, I	o	co
Pentatomidae					
Aelia americana Dallas	a	f, l	C, I	p	co
Rhytidilomia uhleri Stal	a	f	C, I	o	co
COLEOPTERA					
Elateridae					
Anchastus cinereipennis Eschscholtz	l	r	C, I	o	co
Cardiophorus sp.	l	r	C	u	co
Limonius infuscatus Motschulsky	l	r	C	o	co
Limonius sp.	l	r	I	u	co
Melyridae					
Attalus glabrellus Fall	a	f	I	p	co
Attalus morulus smithi Hopping	a	f	I	p	co
Collops bipunctus (Say)	a	f	I	p	co
Anthicidae					
Notoxus serratus LeConte	a	f, s	C, I	p	co
Phalacridae					
Phalacrus pencillatus Say	a	f	C, I	p	co
Scarabaeidae					
Dichelonyx sp.	l	r	C	u	co
	a	c, l	C	u	co

Table 1 continued.

Taxa	Life stage[a]	Plant parts[b]	Location	Host spec.[c]	Abundance[d]
Cerambycidae					
Cortodera barri Linsley & Chemsak	l	r	C, I	o	ra
	a	f	C, I	p	co
Chrysomelidae					
Altica sp.	a	f	C, I	u	co
Anisostena californica Van Dyke	a	l	C, I	o	co
Curculionidae					
Brachyrhinus ovatus (Linnaeus)	a	r	C	p	co
Sphenophorus gentilis LeConte	l	r	I	o	—
	a	s	I	o	co
LEPIDOPTERA					
Noctuidae					
Faronta diffusa (Walker)	l	f, s	C, I	o	co
HYMENOPTERA					
Cephidae					
Cephus cinctus Norton	l	c(i)	C, I	o	co
Eurytomidae					
Tetramesa elymophaga (Phillips)	l	c(i)	C, I	m	co
Tetramesa sp.	l	c(i)	C, I	u	co

[a] n = nymph, l = larva, a = adult.
[b] c = culm, l = leaf, r = root, f = flower, s = seed, (i) = internal.
[c] p = polyphagous, o = oligophagous, m = monophagous, u = unknown.
[d] ra = rare (fewer than 10 insects collected), un = uncommon (10–50 insects collected), co = common (more than 50 insects collected).

TABLE 2. Insect parasitoids reared from insect hosts in Great Basin wildrye culms collected from Craters of the Moon National Monument (C) and the Idaho National Engineering Laboratory (I) in 1983.

Taxa	Host	Location
HYMENOPTERA		
Eulophidae		
Pediobius utahensis (Crawford)	*Cephus cinctus* Nort.	C, I
Zagrammosoma nigrolineatum Crawford	unknown[a]	I
Eupelmidae		
Calosota sp.	*Tetramesa* sp.	I
Torymidae		
Torymus thalassinus (Crosby)	*Tetramesa* sp.	I
Pteromalidae		
Homoporus atriscapus Gahan	unknown[b]	C
Homoporus sp.	*Tetramesa* sp.	C
Eurytomidae		
Eurytoma pachyneuron Girault	*Tetramesa* sp.	C
Eurytoma sp.	*Tetramesa* sp.	C, I

[a] Previously reported to be a parasite on *Argyresthia* sp. (Lepidoptera: Yponomeutidae) (Krombein et al. 1979).
[b] Probably parasitic on *Tetramesa* sp.

grass tiller. Less common were the scales found on the stems under the leaf sheaths. Impacts from these Homoptera could not be separated from the damage due to the fluid-feeding hemipterans.

Many species of mirids cause injury to range grasses through toxemia and loss of plant fluids (Watts et al. 1982). *Irbisia pacifica*, *Litomeris debilis*, and *Stenodema laevigatum* frequently fed on wildrye at both sites. In June 1983 at CRMO, a large section of the study site was observed turning brown. Basin wildrye plants were stunted in the four-leaf stage by infestations of the black grass bug, *Labops utahensis*, and the delphacid *Eurysa obesa*. When insect numbers declined later in the summer, wildrye resumed growth but did not produce any reproductive tillers. Adequate soil moisture and carbohydrate reserves may have enabled the plants to recover. However, the black grass bug can significantly reduce forage production and may cause death if droughty conditions prevail (Todd and Kamm 1974, Haws 1978).

TABLE 3. Sorensen coefficients of insect community similarity by guild on Great Basin wildrye at Craters of the Moon National Monument (CRMO) and the Idaho National Engineering Laboratory (INEL) in 1982 and 1983.

Guilds	Number of species CRMO	INEL	Common	SI[a]
Fluid-feeders—roots	2	2	0	0.00
Chewers—roots	3	2	1	0.40
Fluid-feeders—leaves & culms	14	11	8	0.64
Chewers—leaves & culms	10	4	3	0.43
Fluid-feeders—flowers & seeds	5	4	4	0.89
Chewers—flowers & seeds	2	3	2	0.80
Internal chewers—culms	3	3	3	1.00
Internal parasites	5	5	2	0.40
Pollen feeders	6	9	6	0.80
Total species[b]	45	38	26	0.62

[a] $SI = \frac{2\,(\text{Common})}{\text{CRMO} + \text{INEL}}$ (Sorensen 1948, Wolda 1981).

[b] Columns do not add up to total because some insects overlap guilds.

Flower- and Seed-Feeders

Thrips, pentatomids, adult beetles, and larvae of a species of Lepidoptera were collected on wildrye inflorescences. Seven species of beetles consumed the pollen. Most of these beetles were polyphagous herbivores that switch hosts to take advantage of the available nutritious food source (Thomas and Werner 1981). This may also have been true of the pentatomids that were found feeding on the developing seeds. However, adult billbugs seemed to be monophagous on wildrye in this area. They were observed chewing on the developing seeds of *Elymus*. After seed maturation, adult billbugs were no longer observed. Thrips were collected throughout the season. Two families and six species of Thysanoptera were represented in the Great Basin wildrye insect community. *Frankliniella occidentalis*, the western flower thrip, is a widespread, generalist feeder that has previously been reported on grasses (Tingey et al. 1972, Watts and Bellotti 1967, Knowlton and Thomas 1933). Thrips are often cited as causing damage to grass seed (Thomas and Werner 1981, Riherd 1954, Bailey 1948). The only lepidopteran associated with wildrye, *Faronta diffusa*, fed on the inflorescences at both sites. This species is especially destructive to wheat, oats, and rye (Walkden 1950) and has been reported on a variety of native grasses in Arizona, New Mexico, and Utah (Godfrey 1972, Watts and Bellotti 1967).

Parasites

Eight chalcid parasitoids (Hymenoptera: Chalcidoidea) were reared from insect hosts in Great Basin wildrye culms. *Pediobius utahensis* was reared from sites of developing wheat stem sawflies in stubs of wildrye culms. The other chalcid parasitoids were collected within the culms in the second, third, and fourth internodes and were associated with *Tetramesa* species. It is not known whether any of these wasps were hyperparasites.

Herbivore Guild Complexity

Twenty-six of the 46 insect species collected on basin wildrye were found at both the CRMO and INEL sites (Table 3). Presence or absence of a species was utilized as an indicator of insect fauna similarity between sites. Similarity indices were estimated using Sorensen's (1948) coefficient (Wolda 1981). Each guild was examined individually. Internal chewers and flower and seed feeders displayed the greatest similarity. The small number of grasshopper species at the INEL site may account for differences in leaf and culm external chewers. Low similarity indices for root insects may reflect the very different soil types of the two stands. Although occurring only 40 km apart, the CRMO and INEL sites are different habitat types and represent the wide ecological amplitude of basin wildrye. Climatic and edaphic differences may account for much of the difference in insect species collected from each site.

The majority of the species that constitute the wildrye herbivore guilds are oligophagous, also feeding on cultivated grains as well as other native and introduced grasses. Rangelands are thought to be a source of most insect pests of cereal grains (Watts et al. 1982).

Wildrye, a large, structurally diverse plant, supports a sizable fauna and thus may serve as a reservoir for many of these herbivores. However, wildrye stands also may function as reservoirs for potentially useful predator and parasite species.

The number of phytophagous insect species exploiting Great Basin wildrye was quite large relative to other native grasses in the area. Very few studies have identified the total phytophagous insect community associated with an individual grass species. Watts (1963) collected 120 species on black grama grass, *Bouteloua eriopoda* Torrey; however, these included grass-feeders, parasites and predators, and casual visitors. Wight (1986) identified 33 phytophagous insects on the introduced crested wheatgrass, *Agropyron cristatum* (L.) Gaertn., in southern Idaho. Beisler and his colleagues (1977) collected phytophagous insects associated with three weedy grasses. They found 33 species feeding on Johnson grass, *Sorghum halepense* (L.) Pers.; 39 on fall panicum, *Panicum dichotomiflorum* Michx.; and 35 associated with large crabgrass, *Digitaria sanguinalis* (L.) Scop.

Plant structural diversity, species area relationships, and taxonomic isolation are thought to explain much of the richness of insect species on a host plant (Lawton and Schroder 1977, Southwood 1961, Strong and Levin 1979). Grasses and forbs are less structurally diverse than trees and shrubs and usually have fewer associated species (Niemela et al. 1982, Strong et al. 1984). However, wildrye's height and foliage diversity provide a greater variety of microhabitats than do most range grasses. Tallamy and Denno (1979) found the more structurally complex grass *Distichlis spicata* (L.) Greene supported a richer community of sap-feeders than the simpler *Spartina alterniflora* Loisel.

Taxonomically isolated plants may have impoverished insect faunas (Strong et al. 1984). Wildrye belongs to the grass tribe Triticeae. Idaho is included as one of the areas of the world with the greatest concentrations of species in this tribe (Hartley 1972). Therefore, many closely related grass genera, such as *Agropyron*, *Sitanion*, and *Hordeum*, are well represented in the area. Many insects that feed on wildrye are likely to feed on alternate hosts in related genera, thus increasing the geographical area they may exploit.

Insect species found on a particular host plant are influenced by the local abundance of the plant, both its density and extent (Strong et al. 1984, Fowler and Lawton 1982, Root 1973). On the study sites wildrye grew in almost pure stands, but in very different habitats. Wildrye has a large geographic range, grows in a variety of habitat types (Walker and Brotherson 1982), and is locally abundant within these types. Insects feeding on this grass find a large, conspicuous food source that remains available longer into the summer than any other C_3 grass species in the area.

Graminivorous insects were identified that have the potential to reduce forage and seed production of wildrye. This information may be valuable to grass breeders, seed companies, and range managers interested in revegetation of certain types of rangelands with basin wildrye. Some of the phytophagous insects in this study apparently reduced reproductive potential of wildrye and may have detrimental effects on reseedings. Although grasses are very tolerant of herbivory and have evolved many means of tolerating grazing (McNaughton 1979, Stebbins 1981), insect populations fluctuate greatly and in some years could reach injurious levels. Therefore, it is important to identify which plants and plant parts are fed upon by various members of the insect community and to determine the impact of herbivory on an individual plant species and its population dynamics.

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EFFECTS OF FOREST FUEL SMOKE ON DWARF MISTLETOE SEED GERMINATION

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ABSTRACT.—Seeds of three species of dwarf mistletoe, *Arceuthobium americanum* Nutt. ex Engelm., *A. cyanocarpum* Coulter & Nelson, and *A. vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens, were exposed to smoke from burning forest fuels. Premeasured amounts of coniferous needles and branch wood were burned in a small incinerator with smoke passing through a closed chamber containing the seeds. Following three different smoke treatments and one high-temperature treatment, tests were conducted to evaluate the effects of these treatments on seed germination. Germination was inhibited for all species when the seeds were exposed to smoke for 60 minutes or longer. Seeds of *A. americanum* were unaffected by exposures of up to 40 minutes from fuels with high moisture contents, but enhanced germination occurred after 30 minutes of exposure to smoke from drier fuels. The percentage of germinating seeds of *A. cyanocarpum* and *A. vaginatum* showed little effect from exposures of up to 30 minutes.

Dwarf mistletoe species (*Arceuthobium* spp.) are the most serious of diseases in coniferous forest communities of western North America (Alexander and Hawksworth 1975). These plants are obligate parasites that attack specific coniferous host tree species and appropriate water, minerals, and other nutrients from the host. Injury to infected trees results in a continual reduction of host assimilatory leaf-surface area (Weir 1916, Korstian and Long 1922), decreased growth, reduced vigor, and increased mortality (Hawksworth 1961, 1975, Wicker and Leaphart 1976). Hawksworth and Wiens (1972) discuss dwarf mistletoe biology and host reaction extensively.

Wildfires, which occurred repeatedly in coniferous forest communities prior to the advent of organized fire suppression (Weaver 1951, Wellner 1970, Arno 1976, McBride and Laven 1976, Stokes and Dieterich 1980), are a major ecological force that influenced forest structure and development and also significantly affected dwarf mistletoe population dynamics (Gill and Hawksworth 1964, Baranyay 1970, Wicker and Leaphart 1976, Tinnin 1981). Fire affects dwarf mistletoes directly by killing and consuming host tissues and parasitic plants. These effects are dramatic, immediate, readily observable, and well known. The indirect relationships of fire to dwarf mistletoes, such as reduction of growth or vigor in hosts and parasites, loss of parasite seed viability, or predisposition of hosts to other damaging agents, may be caused by exposure to smoke or elevated temperatures. These effects are subtle, gradual, and difficult to observe. The effects of forest fire smoke exposure on dwarf mistletoe growth and development are unknown and constitute an area of necessary research (Alexander and Hawksworth 1975, Hardison 1976, Koonce and Roth 1980, Smith 1981).

Several workers have reported the effects of smoke on various disease-causing agents. Long (1922) observed that mistletoe (*Phoradendron* spp.) parasitizing one seed juniper (*Juniperus monosperma* [Engelm.] Sarg.) died after exposure to smelter smoke. Spore germination, mycelial growth, and infection of several species of fungi are inhibited after exposure to pine needle and grass smoke (Parmeter and Uhrenholdt 1975). Koonce and Roth (1980) suggested that heat and smoke may affect dwarf mistletoe plants (*Arceuthobium campylopodum* Engelm.) more severely than the associated host plants (*Pinus ponderosa* Laws.).

This study will improve our understanding of the indirect relationships of fire and dwarf mistletoe. The primary objective was to evaluate the effects of various durations of forest fuel smoke exposure on seed germination of three dwarf mistletoe species.

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MATERIALS AND METHODS

Dwarf mistletoe, *A. americanum*, seeds were collected from lodgepole pine (*Pinus contorta* Dougl.), *A. cyanocarpum* were collected from limber pine (*Pinus flexilis* James), and *A. vaginatum* were collected from ponderosa pine in a manner similar to that discussed by Scharpf and Parmeter (1962). These seeds were then placed in petri dishes (50 per dish) and stored in a refrigerator at 6 C for equal time periods until ready for treatment.

A smoking apparatus, similar to that described by Parmeter and Uhrenholdt (1975), was constructed from a small wood stove, uninsulated duct pipe, and a refrigerator. Smoke from burning fuels in the wood stove passed into a 10-cm-diameter duct pipe and traveled 5.5 m through this uninsulated pipe to allow cooling and to minimize heat effects. The pipe entered the bottom of the refrigerator, permitting smoke movement through shelves supporting the petri dishes upward and outward through the refrigerator roof. Use of wire mesh shelves and a small electric fan promoted a somewhat even distribution and movement of smoke through the chamber.

Three smoke treatment experiments were conducted. First, samples of seeds of all three dwarf mistletoe species were exposed to smoke for 0 (control), 60, and 180 minutes. Second, samples of all three species were exposed to smoke for 0, 1, 5, 15, and 30 minutes. Third, samples of only *A. americanum* seeds were exposed to smoke for 0, 10, 20, 30, 40, 50, 60, and 90 minutes.

Ponderosa pine, lodgepole pine, and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) needles and branch wood were used to generate smoke. This fuel was collected from the forest floor duff layer. Moisture content and weight of fuels consumed were determined prior to each experiment. Air temperatures inside and outside the smoking chamber were recorded during the exposure periods. Chemical composition of smoke was analyzed for polynuclear aromatic hydrocarbons (PAH), a common pollutant in combustion emissions. Analysis methods are reported in Tan et al. (1985).

Separate germination tests were conducted with *A. americanum* seeds in an attempt to assess the effects of high temperatures on germination. Only *A. americanum* seeds were used in this test as well as in the third smoke treatment experiment because seeds of the other species were not available in sufficient quantities for collection and treatment. The *A. americanum* seeds were exposed to elevated temperatures for selected time periods in a portable heating apparatus.

The heat treatment chamber was constructed of lightweight aluminum and insulated with 2.54-cm insulation board. A small electric fan was attached to the bottom of the box along with the heat source, a 750-watt ceramic heating coil screwed into a 110-volt electric light socket. An aluminum shelf, insulated on the upper side, was placed directly above the heating element to shield petri dishes and dwarf mistletoe seeds from direct heat. This shelf was open on both sides, and the continuously operating fan promoted movement of heated air around the shield into the space occupied by the dishes and seeds.

Air temperatures inside the treatment chamber were controlled by a separate control box. This device possessed time and temperature control features which enabled the setting of a desired temperature and time period on the dial panel. The control box automatically activated the heating element as needed to attain the desired temperature. After the preset temperature was achieved, the timer engaged and the heating element operated as needed to maintain the internal temperature. Following operation for the preset time period, the control box disengaged both the timer and the heating element, allowing the chamber to cool down. A solid-state, two-terminal, integrated circuit temperature transducer attached to the control box circuit board monitored the chamber air temperature. This transducer permitted the control box to maintain the chamber temperature within ± 0.5 degrees C. A thermometer placed inside the treatment chamber provided a check of the temperature controller.

Elevated temperature treatments included time periods of 30 and 45 minutes for both 35 and 40 C, and 2, 5, and 10 minutes for 45 and 50 C. An unexposed group was used for comparison. These temperatures and durations were selected to correspond to the temperature environments within the smoke treatment chamber during smoke experiments.

TABLE 1. Air temperature (°C) during smoke treatment experiments.

Experiment number	Temperature[1] location	Time (minutes)													
		0	1	5	10	15	20	30	40	50	60	90	120	150	180
1	0	12	—	—	—	—	—	—	—	—	12	14	13	12	12
	I	17	—	—	—	—	—	—	—	—	40	40	43	46	41
2	0	17	17	17	—	19	—	21	—	—	—	—	—	—	—
	I	21	21	21	—	23	—	31	—	—	—	—	—	—	—
3	0	10	—	10	11	12	13	16	18	18	18	23	—	—	—
	I	9	—	25	30	35	32	35	37	37	38	44	—	—	—

[1] Temperature locations are signified as 0 = outside ambient air temperature, I = air temperature inside smoke treatment chamber.

TABLE 2. Average percent germination of *A. americanum* seeds after exposure to temperatures and durations that occurred during smoke treatments.

Temp (°C)	Time (minutes)				
	2	5	10	30	40
35	—	—	—	35.6	18.8
40	—	—	—	38.8	6.4[3]
45	30.8	28.8	26.4	—	—
50	50.8[2]	24.0	6.0[3]	—	—

[1] Average germination of the untreated group used for comparison = 26.8%.
[2] Average percent germination significantly higher than untreated group.
[3] Average percent germination significantly lower than untreated group.

After exposure to smoke or high temperatures, treated and untreated seeds were immersed in a 2% hydrogen peroxide solution to inhibit fungal attack and facilitate maximum germination (Wicker 1974). The seeds were then placed in a standard germination chamber for 30 days and maintained at 16 C with an 8-hour light treatment during each 24-hour period. A visible radicle that ruptured the endocarp was taken as positive evidence of germination (Knutson 1969). Statistical analyses that compared average percent germination of treated and untreated groups were conducted with one-way analysis of variance and Duncan's Multiple Range Test. The .05 level of statistical probability was selected as significant.

RESULTS

During the initial experiment, 3,235 g of fuel averaging 8% moisture content (oven-dry basis) was consumed. In the second experiment, 1,816 g of fuel having a moisture content of 25% was burned, while in the final experiment 4,225 g of fuel with an average moisture content of 34% was consumed.

Maximum air temperatures outside the treatment chamber varied from 12 to 23 C for the three experiments (Table 1). Inside chamber temperatures showed a gradual increase in all experiments, with the maximum reaching as high as 46 C (Table 1). Although inside air temperatures exceeded outside air temperatures throughout most of the experiments, the maximum inside temperature persisted for a relatively short time.

Analyses of smoke particulates to assess PAH composition were conducted on both the wood and duff fuel used in the study. Composition of PAH from wood burning was found to resemble that from other environmental samples such as air particulates and sediments where parental PAH are the predominant components (Tan et al., unpublished manuscript). Duff burning, however, illustrated a PAH composition markedly different from the composition in environmental samples such as air, sediments, and wood-burning emitted particulates.

In typical environmental samples, parental PAH generally make up the major components. In smoke particles from duff burning, phenanthrene, alkylated phenanthrene, alkylated cyclopenta(def)phenanthrene, and dodecahydrochrysene clearly stood out as the predominant components (Tan et al., unpublished manuscript). In addition, the concentration of individual PAH in smoke particles varied with moisture content of burning duff, but not in a systematic way for all components (Tan et al., unpublished manuscript). No ready explanation is available for this occurrence.

Exposure of dwarf mistletoe seeds to elevated temperatures for different periods of time resulted in variable seed germination (Table 2). While average percent germination of seeds did not continually decrease as time and temperature increased, it was lowest after treatment. After heating at temperatures of 40

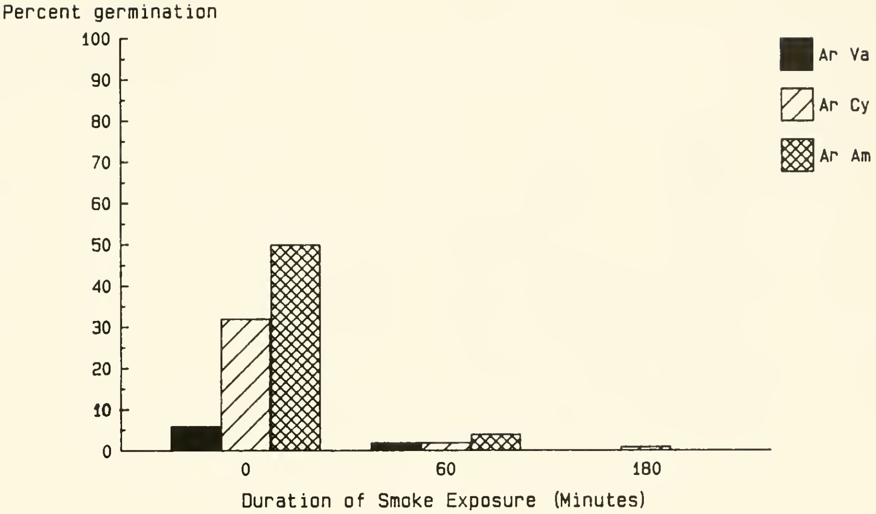

Fig. 1. Average percent germination of *Arceuthobium vaginatum* (Ar Va), *A. cyanocarpum* (Ar Cy), and *A. americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 25% moisture content.

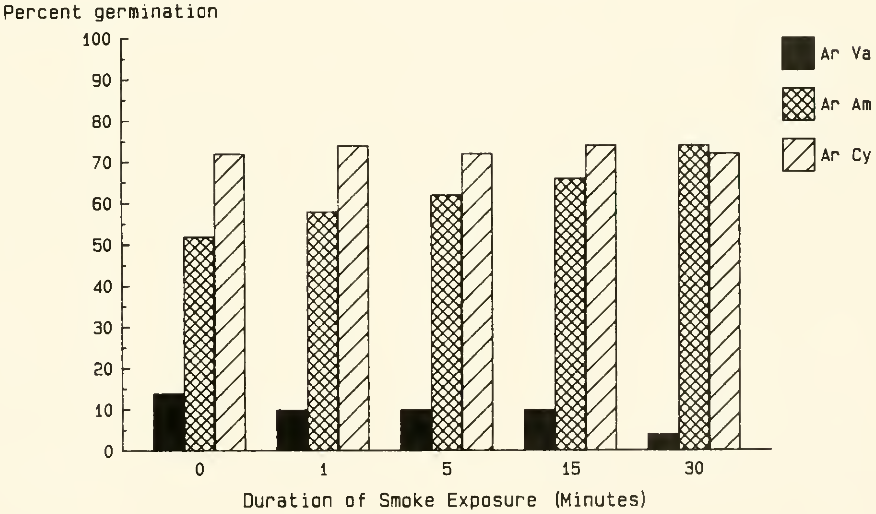

Fig. 2. Average percent germination of *Arceuthobium vaginatum* (Ar Va), *A. cyanocarpum* (Ar Cy), and *A. americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 8% moisture content.

C for 40 minutes, average percent germination was significantly reduced (Table 2). Germination was unaffected when exposed to 45 C. Treatment at a still higher temperature (50 C) appeared to stimulate germination at low durations (2 min), while inhibiting germination after 10 minutes (Table 2).

Exposure of dwarf mistletoe seeds to different smoke durations caused varying results, depending on the moisture content of the fuels consumed (Figs. 1–3). Average percent seed germination of all dwarf mistletoe species was markedly reduced after smoke exposure of 60 minutes or more regardless of the fuel moisture content (Figs. 1, 3).

Average percent germination of *A. americanum* seeds varied with both duration of smoke exposure and fuel moisture content (Figs. 1–3). Smoke exposure of 20 minutes or less had no effect on germination in all

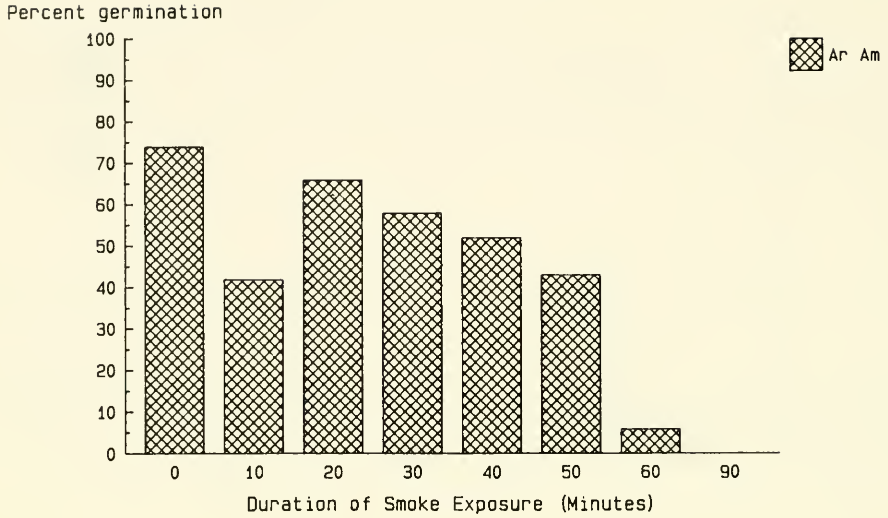

Fig. 3. Average percent germination of *Arceuthobium americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 34% moisture content.

experiments except that exposure to smoke from moist fuels for 10 minutes resulted in significantly lower average percent germination (Fig. 3). However, this trend was not consistent because both untreated seed groups and groups exposed for longer duration had significantly higher germination percentages (Fig. 3). This apparent anomaly may have resulted from factors other than exposure to forest fuel smoke. Exposure of seeds of this species to smoke for 30 minutes from fuels with a low moisture content resulted in average percent germination levels significantly higher than seeds in the unexposed group (Fig. 2). However, 30 minutes of smoke exposure from fuels with high moisture contents resulted in no significant differences in average percent germination (Fig. 3). Exposure to smoke from fuels with high moisture content for longer than 40 minutes caused a significant decrease in the germination of *A. americanum* seeds (Fig. 3). The percentage of germinating seeds exposed to 60 minutes of smoke was less than one-twelfth of the average germination for the untreated groups in both the first and third experiments (Figs. 1, 3). No *A. americanum* seeds germinated after smoke exposure reached 90 minutes (Figs. 1, 3).

Average percent germination of *A. cyanocarpum* seeds exposed to smoke for 0, 1, 5, 15, and 30 minutes did not differ markedly (Fig. 2). However, average percent seed germination was significantly reduced after exposure to smoke for at least 60 minutes (Fig. 1).

Germination percentages of *A. vaginatum* were considerably lower than those of the other species for all treatments including the controls (Figs. 1, 2). Germination of *A. vaginatum* seeds decreased slightly as smoke exposure increased but was not significant until exposure periods exceeded 30 minutes.

DISCUSSION

Substantially lower seed germination percentages of all dwarf mistletoe species when smoke exposures exceeded 30 minutes may result from several factors: (1) a threshold level of smoke toxicity to seeds, (2) chemical toxicity of various fuel types, (3) temperature, and (4) lack of air mixing around the plants.

The occurrence of PAH in the combustion products of carbonaceous fuels agrees with Sandberg et al. (1979). In a study of PAH production from laboratory burning of pine needles with moisture contents ranging from 18 to 27%, McMahon and Tsoukalas (1978) report that heading fires appear to produce higher total particulate matter but lower PAH values than backing fires. Within heading fires, PAH levels also vary as the fire phase varies. Flaming phases produce lower levels of both total particulate matter and PAH than smoldering phases. Specific causes of these effects are hard to pinpoint, but apparently the longer residence times associated with backing and smoldering fires are more conducive to PAH-compound formation.

Increasing moisture in fuels should result in lower combustion efficiency, thereby increasing residence time and PAH production. But, fuels burned with the lowest moisture content (8%) caused the greatest total PAH production (Tan et al., unpublished manuscript). Total PAH production was lowest in smoke produced from the fuels having the highest moisture content. Since individual PAH concentrations varied in an unsystematic fashion as fuel moisture content increased, the influence of specific compounds on seed germination appears to be more important than the influence of total PAH production.

Exposure duration is a major factor determining the degree of injury from compounds contained in or formed as a result of smoke (Jensen and Dochinger 1974, Dochinger and Jensen 1975). Smoke contains or results in formation of numerous compounds, primarily oxidants (Cramer 1974, Evans et al. 1977), which are toxic at relatively low levels to vegetation. Smoke in low doses can have minor effects on plant physiological processes, while high doses can result in acute toxicity and tissue necrosis (Sandberg et al. 1979).

Structure of the smoke treatment chamber failed to remove all possible effects of high-temperature exposure on seed germination. Separate tests completed with the heating apparatus, however, did effectively isolate this source of variation. Average percent germination of those seeds exposed only to elevated temperatures did not follow any consistent trends. Although differential viability may have been responsible for these inconsistencies, it was not assessed in either the smoke or temperature treatments. The fact that differential viability had an equal probability of influencing the percent of seeds germinating after exposure to smoke or high temperatures indicates that it had little effect on the observed outcome.

Seeds exposed to temperature environments in the heating apparatus (which correspond to temperature environments within the smoke treatment chamber) showed reductions in average percent germination only after long exposure. Thus, it appears that at these temperatures for exposures of less than 60 minutes, smoke was the major factor influencing dwarf mistletoe seed germination. As exposure exceeded 60 minutes, the temperature treatment became an increasingly important factor affecting seed germination. After longer durations (90 minutes), the combined effects of the temperatures used in this study and smoke appear lethal to dwarf mistletoe seeds.

Average percent germination of *A. vaginatum* seeds was significantly lower than the other species for all treatments, including the control. Conceivably, lower germination percentages of *A. vaginatum* seeds may indicate that the other species have evolved ecological adaptations to smoke exposure. Seeds of *A. vaginatum* commonly mature four to six weeks before the seeds of *A. americanum* and *A. cyanocarpum*. Upon reaching maturity, *A. vaginatum* seeds are expelled from the fruit and germinate within a short period of time. Seeds of *A. americanum* and *A. cyanocarpum* mature in late August or early September and are expelled onto the host material. They then overwinter on the twig and germinate the following May. Consequently, *A. vaginatum* seeds are susceptible to smoke exposure for a much shorter period of time than those of the other species. Frequent smoke exposure may have permitted seeds of *A. americanum* and *A. cyanocarpum* to evolve mechanisms that promote successful germination in the presence of smoke of low concentrations for short durations.

SUMMARY

Fire is one of the principal agents preventing parasitic species from overrunning host populations (Tinnin 1981). Smoke from fire is a common occurrence in many coniferous forest communities. Although the preservative properties of smoke are well known (Frazier 1967), the specific effects of smoke exposure on dwarf mistletoe growth and development have not been documented.

Results reported here indicate that prolonged smoke exposure inhibits dwarf mistletoe seed germination. After continuous exposure for more than 60 minutes, smoke, and the accompanying increase in temperatures, both severely limit dwarf mistletoe seed germination. Brief exposure to smoke from fuels with low moisture contents causes increased germination of *A. americanum* seeds but has little effect on *A. cyanocarpum* and *A. vaginatum* seed germination.

Other relationships between fire and dwarf mistletoes are still not well understood. Fumigation of coniferous forests by smoke from wildfires may affect plant development, pollination, fruit maturation, and infection by dwarf mistletoes. Smoke may have secondary effects on these parasites by affecting host vigor.

Although this paper by no means addresses all of the relationships between fire and dwarf mistletoe, it does provide new ecological information concerning the effects of forest fuel smoke on dwarf mistletoe seed germination.

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MICROVELIA RASILIS DRAKE IN ARIZONA: A SPECIES NEW TO THE UNITED STATES (HETEROPTERA: VELIIDAE)

John T. Polhemus[1] and Milton W. Sanderson[2]

ABSTRACT.—*Microvelia rasilis* Drake was taken in Montezuma Well, Yavapai Co., Arizona, along with *Microvelia hinei* Drake and *Hydrometra aemula* Drake (Heteroptera: Hydrometridae). These are all new to this locality; however, the latter two species are previously known from Arizona.

Recently we collected some *Microvelia* from Montezuma Well, Yavapai Co., Arizona, expecting that they would be *M. hinei* Drake 1920. Subsequent examination revealed two species, *M. hinei* and *M. rasilis* Drake 1951. In his revision of the genus, Cecil Smith (1980, A taxonomic revision of the genus *Microvelia* Westwood [Heteroptera: Veliidae] of North America including Mexico, unpublished dissertation, University of Georgia, Athens, xv + 372 pp.) treated *rasilis* as a species only provisionally distinct from *hinei*. However, in the sample from Montezuma Well the two are distinct and easily separable by Smith's key characters. In *hinei* the dorsum of the thorax appears two-segmented with the mesonotum completely covered by the pronotum, the last two abdominal tergites have narrow, longitudinal median shining areas, the coloration is yellowish with rather extensive, dark markings on the thorax and abdomen, and the size is distinctly smaller than *rasilis*. In *rasilis* the mesonotum is narrowly but distinctly exposed, the abdominal tergites are without median shining areas, the coloration is mostly light yellowish, and the size is distinctly larger.

Microvelia hinei is a common, quite variable species widely distributed in the United States and Mexico, reaching Argentina to the south, and previously known from several locations in Arizona (Smith 1980). On the other hand, *M. rasilis* is quite rare, known only from a few specimens, which led Smith to question its specific distinctness from *hinei*. The presence of the two at one locality removes that doubt. The closest previous collection locality for *rasilis* was Telonzo, Michoacán, Mexico, 12-IV-1975, CL741, by J. T. Polhemus in a spring-fed pool among water hyacinths; this locality is about 1,900 km south of Montezuma Well. Other specimens in the Polhemus collection are from the Mexican states of Mexico and Puebla.

Collection data for the Montezuma Well specimens are: *M. hinei:* 2 ♂, 1 ♀, 8-VII-1986, MWS; 7 ♀, 21-V-1987, MWS and JTP; 2 ♂, 8 ♀, 8-VI-1987, MWS. *M. rasilis:* 2 ♀, 21-V-1987, JTP; 1 ♀, 8-VI-1987, MWS.

The Montezuma Well collection of 21-V-1987 also includes *Hydrometra aemula* Drake 1956, a species distributed in western Mexico and Arizona, but not previously known from this locality.

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